ENVIRONMENTAL PREDICTORS OF BOTTLENOSE DOLPHIN DISTRIBUTION AND CORE FEEDING DENSITIES IN GALVESTON BAY, TEXAS

A Dissertation

by

MARIA PAULA TEIXEIRA MORENO

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2005

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

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ABSTRACT

Environmental Predictors of Bottlenose Dolphin Distribution and Core Feeding Densities in Galveston Bay, Texas. (May 2005)

Maria Paula Teixeira Moreno, M.S., Universidade de Lisboa, Faculdade de Ciências

Chair of Advisory Committee: Dr. Bernd Würsig

Coastal dolphins are often exposed to habitat degradation and direct interactions with humans. Major factors that influence dolphin distribution, critical for conservation concerns, are still poorly understood even for the bottlenose dolphin, the best-studied cetacean. To establish the environmental conditions that best predict occurrence of bottlenose dolphins and high feeding densities in Galveston Bay, I conducted a total of 367 boat surveys in five locations of the estuary, totaling 3,814.77 km of search effort. I counted groups of dolphins and measured surface water temperature, salinity, turbidity, total number of boats, shrimp vessels, and number of seabirds. Using geospatial tools, these data -- along with location, distance to the Gulf of Mexico and water depth -- were analyzed on a 500-m resolution grid. Temporal factors at daily and seasonal scales were also examined. Occurrence was modeled using a Generalized Additive Model and core feeding densities (i.e., feeding densities above 2 SD of the mean) were modeled with a Generalized Linear Model. A total of 1,802 dolphins in 262 groups were detected, 56.87% of which were feeding. I found that all factors except warm/cold seasons and turbidity were useful to predict dolphin distribution, which was related non-linearly to most predictors. Fewer variables were relevant in predicting core feeding densities. These were, in decreasing order of relevance, distance to the Gulf of Mexico, surface water temperature, depth, number of boats, and warm/cold seasons. Feeding was highly clustered and the main core areas, less than approximately 3 km^2 wide, were stable across time of day and season. The majority of the occurrences (86.2%) and feeding groups (94%) were situated in two bay locations - Galveston Ship Channel (GSC) and Bolivar Roads (BRD) - that amounted to only one-fifth of the surveyed area. Compared to conditions in GSC and BRD when no dolphins were sighted, feeding cores were

deeper and more seabirds were observed. This fine-scale study of bottlenose dolphin distribution may contribute to a better understanding of habitat requirements for coastal dolphins. It also may provide information needed to minimize potential negative impacts to this population caused by human activities.

To my niece Iana Marta Bormann

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TABLE OF CONTENTS

Page

CHAPTER Page

LIST OF TABLES

TABLE Page

LIST OF FIGURES

FIGURE Page

CHAPTER I

INTRODUCTION

Because of generally increasing impact of human activities, the marine environment is suffering changes at multiple levels, resulting in habitat degradation for many species. Cetaceans are particularly vulnerable due to their life-history strategies of being K-selected species, with low fecundity and long gestation periods (Chivers 2002, Taylor 2002). Knowledge of how cetaceans may adapt to environmental changes, such as the drastic depletions of fish stocks, is extremely limited. The need to protect cetacean populations has been recognized at some national and international levels (Reeves 2002). However, most laws are taxon-specific and their success is limited if they do not include habitat protection. Recently, there have been increased recommendations of and designations for Marine Protected Areas that focus on protection of cetacean species (e.g., Wilson *et al*. 1997, Hoyt 2005). Establishing protected areas and, in particular, defining critical habitat, requires additional knowledge about how each species utilizes its habitat, and about the environmental conditions that influences its distribution (Wilson *et al*. 1997, Hoyt 2005).

Knowledge of habitat use patterns is of fundamental importance in identifying relevant environmental determinants of a species' distribution. Typically, the distribution of K-selected species, such as odontocete cetaceans, the toothed whales and dolphins, is more heavily influenced by biotic aspects, namely food and mate availability, than by the physical environment (Pianka 1994). However, quantifying availability of these resources and determining the relative weight of their influence in cetacean distribution is particularly complex. In part, this is because most cetacean species are widely dispersed, most behaviors occur under water, and data concerning distribution of food resources are incomplete.

This dissertation follows the style and format of Ecology.

Attempts to relate the distribution of odontocetes to food abundance are limited mainly to either using non-concurrent measures of prey -- usually at a coarse spatial scale compared to cetacean estimations (Jaquet and Gendron 2002) -- or detailed descriptions of prey distribution, but when these latter measures are available, temporal coverage is limited (Barros and Wells 1998, Benoit- Bird and Au 2003). Despite these logistical limitations, empirical evidence shows that odontocete distribution is often associated with prey density. This is unsurprising since foraging consumes a major proportion of the daily activities of odontocetes (Wells *et al*. 1999).

An alternative approach is to evaluate how odontocete distribution is related to environmental variables that influence prey distribution. Animals use various cues to enhance their foraging efficiency. Delphinids, such as bottlenose dolphins (*Tursiops truncatus*), not only have highly developed visual and acoustical senses that they use in foraging, they also possess a developed cognitive system (Ridgway 1990). The latter assists dolphins both in memorizing previous successes and failures and in establishing associations between environmental conditions and the outcomes of their foraging tactics. As a result, bottlenose dolphins are able to rapidly adjust to changes in their environment, as shown by habituated dolphins that feed in association with shrimp vessels (Fertl 1994a), and those that seek periodic aggregations of fish in tidal fronts (Mendes *et al*. 2002).

Physical variables quantified in relation to delphinid distribution include salinity, water temperature, depth, bottom slope, and distance to the coast. Bathymetry and distance to the coast are commonly found to account for delphinid distribution. However, the relevance of these static variables compared to the influence of other factors may be inflated, since bathymetric and distance variables are more reliably and frequently measured, and fine-scale measurements are easier to obtain.

Although the bottlenose dolphin is probably the best-studied cetacean (Wells and Scott 1997), knowledge about the environmental determinants of its distribution remains limited. This can be attributed partially to their physiological and behavioral flexibility to environmental conditions. Because of this remarkable adaptability, it may be difficult

to tease out the effect of each variable studied, moreover, because most studies address only several factors of many possible ones, it may be difficult to ascertain whether the measured variables are the most relevant ones.

As a species, the bottlenose dolphin occupies a wide variety of environmental conditions, from tropical to temperate latitudes and from offshore to coastal and estuarine habitats.

It is one of the only known delphinids with distinct ecotypes, as shown by the coastal and offshore populations off North Carolina (Torres *et al*. 2003). Coastal populations generally are "fluid" (*sensu* Pianka 1994) showing a high degree of mobility. Home ranges vary depending on the degree of site fidelity, which extends from seasonal to year-round residency (Wells and Scott 1997).

Considering that organisms with large home ranges generally have broader tolerance of variations in environmental conditions, we anticipate that bottlenose dolphins also have typically wide adaptability. However, even bottlenose dolphin populations with large home ranges may not be equally flexible regarding all environmental components. Moreover, trade-offs may occur, when one environmental dimension impacts the tolerance of another (Pianka 1994). This interplay of environmental factors often depends on the organism's reproductive status and activity. For example, cetacean females with calves may more strongly avoid sources of disturbance (Wells *et al*. 1999).

Populations with dissimilar home ranges are likely to exhibit differences in habitat preferences. For example, resident females with offspring (but not nonresident females) tend to occur more often in shallow waters, which offer rich food supplies (Wells 1993) and shelter from predators (Wells *et al*. 1999). However, similarities in environmental correlates also exist among distinct populations. For example, strong associations with currents have been documented among feeding bottlenose dolphins in Moray Firth, Scotland (Mendes *et al*. 2002) and in Sanibel Island, Florida (Shane 1990).

Establishing habitat use patterns is simpler in delphinid species that demonstrate temporal and spatial segregation of their daily activities. The Hawaiian long-snouted spinner dolphin (*Stenella longirostris*) feeds on organisms associated with the deep

scattering layer (DSL) that follow vertical diel movements (Norris *et al*. 1994). Hence, the dolphins' daily activities are synchronized with their prey's vertical movements: resting occurs during the day close to shore in areas protected from predators, and feeding occurs offshore at night. In addition to periodic changes in food availability, the schooling nature of food patches also contributes to synchronizing behaviors among members of the same social group. DSL fish and invertebrates occur in large dense patches that favor coordinated and cooperative feeding in large groups.

In contrast, bottlenose dolphins tend to engage in all activities throughout their home range with apparently little site-specificity. This can be attributed to their generalized feeding habits and opportunistic nature, targeting the most abundant prey species at any given time. Moreover, as is typical of coastal populations, bottlenose dolphins feed on much smaller schools or on non-schooling prey than do dolphins in open waters. In such nearshore instances, cooperative feeding in large groups does not represent the same foraging advantage as it does for dolphins feeding on large schools of fish (Wells *et al*. 1987). In addition, coastal species may take advantage of physiographic features to capture fish, obviating the need for assistance of large groups (Wells *et al*. 1999). Hence, bottlenose dolphins in coastal and estuarine habitats may feed solitarily or in small groups, and feeding may occur concurrently with other activities in the same social unit.

The spatial and temporal segregation of activities is a more recurrent pattern in pelagic species of small odontocetes than in coastal species. Nevertheless, even among coastal species such as the bottlenose dolphin, feeding may occur predominantly at given sites, which may shift seasonally, often suggested to be the result of prey movements (Wells 1993, Maze and Würsig 1999). More studies are needed to elucidate whether site-specific feeding habitats are common for coastal dolphins and to examine the temporal stability of those sites, which would be important targets for conservation.

Feeding habitat, or microhabitat, is likely to occur even in a patchy environment as long as prey occurrence is predictable (Pianka 1994). Coastal bottlenose dolphins spend most of their foraging energy searching for prey. Since a higher density of prey results in a decrease of searching time (Pianka 1994), these dolphins may benefit greatly from

exploiting higher density patches. In favor of this hypothesis is the association of bottlenose dolphins with tidal fronts and shrimp vessels. Foraging dolphins must also spend energy chasing and capturing their prey, and it is likely that tidal fronts and bottom-trawls also facilitate prey capture.

Therefore, I hypothesize that bottlenose dolphins are not found uniformly in estuaries and that feeding is an important daily activity that takes place primarily at predictable sites where prey tends to be found in higher concentrations. This statement translates into the following specific questions:

i) Chapter II – bottlenose dolphin occurrence

Do bottlenose dolphins exhibit site preference in highly dynamic environments such as estuaries? If so, which natural and anthropogenic factors may account for such heterogeneous distribution?

ii) Chapter III – feeding behavior

How important is feeding compared to other activities? What is the contribution of feeding in association with shrimp vessels to the overall feeding? Does feeding occur mainly in given sites? If so, are these "core feeding sites" stable across time? And what factors can best predict dolphin feeding densities in these cores?

As mentioned previously, knowledge about the influence of environmental conditions on occurrence patterns and habitat use of coastal dolphins is still incomplete. Considering that marine mammals are protected under several international agreements and in the U.S. under the Marine Mammal Protection Act (1972), such additional information would be useful for establishing appropriate conservation measures for coastal dolphins.

Bottlenose dolphins are particularly suitable subjects to address habitat use patterns of small coastal delphinids because of:

- Their high behavioral plasticity, particularly regarding feeding modes;
- Their ability to track environmental changes at different temporal scales; and
- The large body of literature on movement patterns and behavior, which paves the way for comparative studies regarding their response to environmental conditions.

Estuaries are unique systems to study habitat requirements of coastal dolphins, in particular the selection of feeding sites, because:

- Estuaries offer a broad range of environmental gradients that can be measured and related to dolphin distribution;
- Their complex habitat structure and occurrence of microhabitats may lead to differential use of habitat by dolphins;
- Estuaries encompass natural and anthropogenic environmental variation, both potential determinants of dolphin distribution;
- Estuaries are important nursery areas for many fish species, thus potentially constituting important feeding grounds for dolphins;
- Estuaries provide dynamic and static features that can aggregate fish, and thus may result in predictable high quality feeding patches;
- Estuaries are well studied, and so baseline information about movement and distribution of fish is available; and
- The fixed geography of estuaries facilitates use of seabirds as proxies for fish abundance.

The Galveston Bay estuary has many advantages facilitating and/or motivating the study of bottlenose dolphin distribution and feeding habitat:

- Bottlenose dolphins are present year-round;
- Bottlenose dolphins engage in two different modes of feeding, feeding in association with shrimp vessels vs. no association;

- Human activities such as bottom-trawling, recreational boating and shipping are intensive but not uniform throughout the bay, thus providing suitable conditions to evaluate their effects on bottlenose dolphin distribution; and
- The Galveston Bay is classified as an estuary of national importance, and specific measures within it to protect the bottlenose dolphin are lacking.

The present study is the first fine-scale spatio-temporal examination of bottlenose dolphin occurrence and feeding that provides predictive models to integrate several anthropogenic and natural environmental variables measured concurrently with bottlenose dolphin behavior and counts over the course of a year, and that analyzes the effects of two temporal scales.

The study is divided into two sections:

Chapter II: Fine-scale environmental predictors of bottlenose dolphin distribution

I investigated whether bottlenose dolphin occurrence in a highly dynamic environment such as the GB is associated with anthropogenic and/or natural environmental conditions.

Selection of variables was based on their perceived potential to influence fish distribution (salinity, water temperature, turbidity, depth, boats, shrimp vessels), the potential for affecting bottlenose dolphin behavior (depth, boats, shrimp vessels), the potential as indicators of fish abundance (seabirds), and as an indicator of home range being contained in the bay, examined as distance to the Gulf of Mexico.

Since distribution may vary at different temporal scales, I analyzed the effect of time of day and seasons on bottlenose dolphin occurrence. Two criteria were used to define season: water temperature and freshwater balance. The latter parameter quantifies the net freshwater in the Galveston Bay after accounting for gains (e.g., precipitation) and losses (e.g., evaporation) (TWDB). I defined warm/cold and wet/dry seasons based on

comparison of observed conditions in this study to mean conditions calculated from a span of five and nine years for temperature and freshwater balance, respectively.

A predictive model of bottlenose dolphin distribution was developed with terms that include both linear and nonlinear responses. Finally, the model predictions are mapped and compared to the observed occurrence pattern.

Chapter III: Environmental predictors of bottlenose dolphin core feeding densities

First, I assessed the importance of feeding in relation to all activities, and compared the relevance of two feeding modes, feeding in association with shrimp vessels vs. feeding without them. Second, I identified the highest feeding density areas (i.e. core feeding densities - CFD), and analyzed their spatial and temporal stability. Next, I determined the relevant environmental predictors of CFD and built a predictive model of CFD distribution.

Given the potential risks of habitat degradation caused by human activities in the Galveston Bay, a set of recommendations was generated to promote conservation of the dolphins in the bay.

CHAPTER II

FINE-SCALE ENVIRONMENTAL PREDICTORS OF BOTTLENOSE DOLPHIN DISTRIBUTION IN THE GALVESTON BAY, TEXAS

SYNOPSIS

An understanding of the factors that determine species distribution patterns is of central importance to species ecology. Although the bottlenose dolphin is one of the best-known species of delphinids, knowledge is scarce about the environmental conditions that may help explain spatial and seasonal movements. Physiography and physical gradients of estuaries offer a unique opportunity to evaluate influences of environmental factors, including human-induced factors, on the distribution of dolphins. I used a generalized additive model (GAM), a modern non-parametric non-linear multiple regression technique, to predict the distribution of bottlenose dolphins in the Galveston Bay estuary. This model integrated environmental and anthropogenic factors. I conducted a total of 367 boat surveys over 124 days from January 22, 2001 to December 29, 2001. This amounted to 3,814.77 km of search effort, yielding a total of 1,802 dolphins in 211 occurrences. I counted groups of dolphins and measured surface water temperature, salinity, turbidity, number of total boats and shrimp boats in particular, and number of seabirds, the latter assumed to be a proxy for prey distribution. Using geospatial tools, the variables -- along with location, distance to the Gulf of Mexico and water depth -- were analyzed on a 500-m resolution grid. Temporal factors at daily and seasonal scales were also examined. I found that all factors except warm/cold seasons and turbidity were useful to predict dolphin distribution in the Galveston Bay. Occurrence of dolphins was linearly and positively correlated with number of seabirds and shrimp vessels; and non-linearly with all other variables. Distance to the Gulf of Mexico was the most influential predictor of occurrence with a peak at about 8 km that corresponds to a zone of confluence. The majority of the occurrences (86.2%) were found in only 21.5% of the total surveyed area. This fine-scale study of bottlenose dolphin distribution may contribute to a better understanding of

habitat requirements for coastal dolphins. It also may provide information needed to minimize potential negative impacts to this population caused by human activities.

INTRODUCTION

Over the past decade, the development of tracking technologies, automated collection of environmental data and geographic information systems, along with the improvement of geospatial analytical tools have greatly facilitated studies of distribution patterns and habitat use of wide-ranging vertebrates. The impact of these technological innovations is particularly evident in the ecological studies of cetaceans: historically, these marine mammals have posed a remarkable challenge to scientific study, due to restricted abilities to undertake direct and continued observations, and to the difficulties inherent in fully characterizing the dynamics of the marine environment at the most appropriate scale (Stern 1998). Moreover, many cetacean species have complex social structures, which makes discerning the factors that determine their distribution particularly daunting.

Despite these difficulties, several studies have linked distribution patterns of both deep water and coastal cetaceans to oceanographic features and environmental conditions. For example, Croll *et al*. (1998) found that off the Californian coast, blue whales (*Balaenoptera musculus*) are more abundant along steep slopes and their distribution is highly correlated with high densities of euphausiids. Similarly, northern bottlenose whales (*Hyperoodon ampullatus*), sperm whales (*Physeter macrocephalus*) and beaked whales (family Ziphiidae) are often found in association with submarine canyons off the Nova Scotia shelf (Whitehead *et al*. 1992, Gowans *et al*. 2000). Higher aggregations of deep water cetaceans were also found to be linked with more dynamic oceanographic features such as warm/cold frontal boundaries formed in the Gulf of Mexico (Ortega-Ortiz 2002, Davis *et al*. 2002) and off Georges Bank (Griffin 1999). Coastal studies have also shown a relationship of cetaceans to bottom topography (Liret and Ridoux 1998, Liret 2001, Hastie *et al*. 2004).

Bathymetric and substrate characteristics are by far the most common attributes found to explain cetacean distribution and habitat preference. These physical factors undoubtedly are an important component of the marine environment that determines or influences distribution of organisms and biological processes. However, as static variables, they also are easier to measure during cetacean surveys or to obtain from other sources. Thus, bathymetric characteristics often are the only oceanographic variable cited in studies of cetacean distribution (e.g., Cañadas *et al*. 2002, Yen *et al*. 2004).

In addition, for most large-scale cetacean studies (embracing areas from 100s km - 1,000s km), a detailed sampling scheme to cover within-season and inter-season variability often is not feasible. This severe limitation of the range of environmental conditions that researchers are able to study may hinder their detection of possible associations with such dynamic variables as water temperature and salinity. Fine-scale surveys have led to discovery of habitat partitioning between cetacean species (Waring *et al*. 2001). Such fine scale surveys undertaken in tandem with collection of several oceanographic parameters have been recognized as necessary vehicles to better understand the ecology and habitat preferences of deep water species (Waring *et al*. 2001). Jaquet (1996) also highlights the influence of spatial and temporal scales in understanding sperm whale and other cetacean distributions.

The study of distribution and habitat use by bottlenose dolphins in estuaries presents a unique opportunity to assess influences of environmental factors at fine temporal and spatial scales. Estuaries are highly dynamic systems with diverse bottom topography and horizontal and vertical physical gradients, factors known to influence species distribution (Alongi 1998, McLusky and Elliot 2004). Bottlenose dolphins inhabit temperate and tropical coastal and oceanic waters (Barros and Odell 1990), and are commonly found in estuaries (Shane 1980, Scott *et al*. 1990, Barco *et al*. 1999, Read *et al*. 2003). Their occurrence in estuaries considerably increases their accessibility for research purposes, compared to most other cetacean species.

Detailed studies of this species in bay and estuarine waters have linked habitat preference to substrate type (Barros and Wells 1998, Allen and Read 2000) and to

physiographic features that are believed to help concentrate prey or facilitate its capture by dolphins (Mendes *et al*. 2002). A fluctuation in bottlenose dolphin abundance in estuarine waters is often hypothesized to be the result of prey movements (Maze and Würsig 1999). This hypothesis has been largely untested because of the difficulty of obtaining complete data on which fish species compose the diet of a generalist species (Bowen and Siniff 1999). Other factors such as predation and calving (Scott *et al*. 1990) have been shown to influence the seasonal distribution of bottlenose dolphins. However, most distribution and habitat studies are limited by the use of fixed environmental variables such as, depth, slope and distance to shore. The few studies that have included non-fixed variables, for example water temperature (Barco *et al*. 1999) and features of estuarine fronts (Mendes *et al*. 2002), found significant correlations of bottlenose distribution with at least some variables.

Despite the broad physiological tolerance of bottlenose dolphins for estuarine environmental gradients, such gradients may well influence the distribution of their prey and thus, at least indirectly, affect bottlenose dolphin distribution. Although characterization of the physical environment may provide useful insights into the distribution of bottlenose dolphins, to my knowledge, no previous predictive model of bottlenose dolphin distribution in estuarine waters integrates dynamic and static hydrographic features measured concurrently with dolphin density estimates. Moreover, most studies of bottlenose dolphins focus on either oceanographic or human-induced features of the habitat (Wells 1993, Allen and Read 2000, Hastie *et al*. 2004). Bottlenose dolphins seem to adapt rapidly to anthropogenic changes, for example by feeding in association with shrimp fisheries (Leatherwood 1975, Shane *et al*. 1986, see review in Fertl and Leatherwood 1997). On the other hand, harmful interactions are also known to occur in estuaries. Vessel traffic is regarded as a source of disturbance to bottlenose dolphins, particularly to females with calves (Wells and Scott 1997, Nowacek *et al*. 2001). In a Gulf of Mexico estuary comparable to Galveston Bay in density of recreational vessel traffic, boats elicit behavioral changes among dolphins, including changes of swimming speed, breathing intervals (Janik and Thompson 1996, Hastie *et*

al. 2003), and group array (Nowacek *et al*. 2001). Consequently, to understand the distribution of bottlenose dolphins in highly modified estuaries, it is essential to address both environmental and anthropogenic variables.

The Galveston Bay estuary is an especially appropriate site for such a fine-scale study, as bottlenose dolphins are common. Since 1990, several studies (e.g. Bräger 1993, Maze and Würsig 1999) have examined distribution and behavior of these dolphins: more than 1,000 individuals have been identified, and it has been estimated that about 200 are year-round residents (Bräger 1993). Studies of occurrence patterns show a substantial increase in numbers of dolphins during summer (Henningsen 1991, Bräger 1992, Fertl 1994a, Maze 1997), and these authors speculated that this pattern reflects prey abundance. However, to date no study has addressed the role of environmental factors. Furthermore, shrimping is intensive in parts of the Galveston Bay, and a high association of dolphins with shrimp vessels has been documented (Fertl 1994b).

In this fine-scale study, I integrate oceanographic factors that are both dynamic (water temperature, turbidity, salinity) and static (distance to ocean waters, depth) with anthropogenic variables (vessel traffic and fisheries) to predict the distribution of bottlenose dolphins in Galveston Bay. I also evaluate the influences of climatic factors (seasons classified according to temperature or freshwater balance), time of day, and location. In addition, I measure seabird density as a proxy for dolphin prey distribution. I hypothesize that spatiotemporal distribution of bottlenose dolphins in Galveston Bay is not uniform and that it may be predicted by one or more environmental and/or anthropogenic variables. I then examine whether predictors used at the scale of the entire study area are also useful for sub-areas. With this multivariate approach, I hope to contribute to a better understanding of bottlenose dolphin distribution in estuaries.

METHODS

Study Area and Data Collection

The Galveston Bay estuary (29°30’ N, 94° 40’ W) encompasses an area of 1,360 km^2 (NOAA 1990) along the upper Texas coast, abutting the Gulf of Mexico (Fig. 1). It

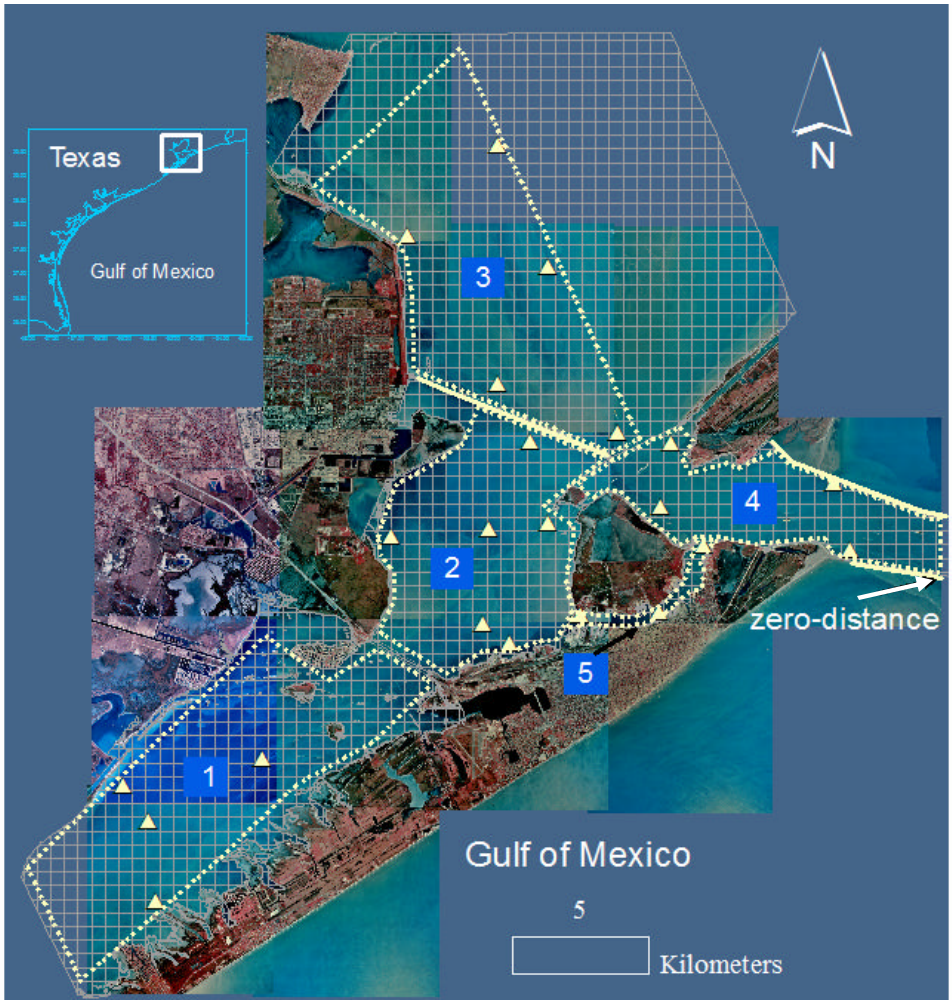

FIG. 1. Location of the study area, Galveston Bay, Texas (square within inset), and the five surveyed locations: West Bay (1), Back Bay (2), Houston Ship Channel (3) Bolivar Roads (4) and Galveston Ship Channel (5), shown within broken lines. Jetties shown as wide, solid lines. The end of the jetties represents the zero-distance (arrow) from the Gulf of Mexico.

consists primarily of shallow, soft bottom embayments averaging 2 m in depth and crossed by a system of channels maintained for navigation by dredging. The main inlet to the Gulf of Mexico (GOM), Bolivar Roads, is jettied and accounts for 80% of the tidal exchange (GBEP 2002). Urban and industrial development, particularly petrochemical refining, is intensive along much of the perimeter of the bay. Other important human activities include recreational and commercial fishing, the latter predominantly for shrimp.

I divided the lower region of the bay into five sections (Fig. 1) to capture environmental (natural and anthropogenic) gradients resulting from physiography and distance to the main inlet to the Gulf. To count dolphins and collect environmental data, I conducted a total of 367 boat surveys over 124 days from January 22, 2001 to December 29, 2001, for a total of 3,814.77 km of search distance. Weather permitting, at least once a month I surveyed each of the five locations at all times of day (Table 1). Time of day was classified into morning, midday and afternoon, each segment corresponding to an equal number of daylight hours. I define a survey as a given combination of date/location/time of day, including partially covered locations. I conducted surveys employing 5 m and 5.7 m outboard vessels along pre-defined routes, stored with GPS, at an average speed of 8 kn (14.4 km/hr). Survey tracks were stored in a Garmin 48 GPS at 1-minute resolution for subsequent estimation of effort and mapping of dolphins and environmental data.

A dolphin group was defined as all dolphins 100 or fewer meters from their nearest neighbor (adapted from Wells *et al*. 1987). Once a group was detected, the search was interrupted to record behavioral data and estimate number of individuals, using scan sampling and instantaneous recording (Martin and Bateson 1993) for five minutes. The encounter rate of dolphins may be severely biased by observers' varying ability to detect them. In order to maintain constant detectability of dolphins, I implemented the following measures: 1) surveys were carried out only below or at sea state 3 (Beaufort scale); 2) one observer covered 90 degrees from the bow to the right and a second observer covered 90 degrees to the left; 3) groups detected while observers followed another group or while they collected environmental data were excluded, and 4) groups detected beyond 200 m from the survey position were excluded *a posteriori* using a buffer in ArcGis 9 (ESRI 2004).

During surveys, I collected environmental data at 22 fixed stations (Fig. 1) and also after following a given dolphin group if it was located more than 500 m from a station or after more than one hour had elapsed following the previous measurement. I measured

TABLE 1. Survey sampling scheme for May 2001.

Date	Location	Time of day
5/2/01	BB	2
5/2/01	BRD	2
5/2/01	GSC	2
5/11/01	BB	3
5/13/01	BB	2
5/13/01	BB	3
5/14/01	BB	2
5/14/01	BB	3
5/14/01	WE	2
5/14/01	WE	3
5/15/01	BB	1
5/15/01	BB	2
5/15/01	HSC	1
5/15/01	HSC	2
5/17/01	BRD	2
5/17/01	BRD	3
5/17/01	GSC	3
5/19/01	BB	2
5/19/01	BB	3
5/19/01	WE	2
5/19/01	WE	3
5/20/01	BRD	2
5/20/01	BRD	3
5/20/01	GSC	2
5/20/01	GSC	3
5/22/01	GSC	2
5/22/01	GSC	3
5/23/01	GSC	1
5/23/01	GSC	2
5/24/01	BRD	3
5/24/01	GSC	2
5/24/01	GSC	3
5/26/01	BRD	1
5/26/01	BRD	2
5/26/01	GSC	1
5/26/01	GSC	2
5/28/01	BB	2
5/28/01	GSC	3
5/30/01	BRD	1
5/30/01	BRD	2
5/30/01	GSC	1
5/30/01	GSC	2
5/30/01	GSC	3

Note: BB = Back Bay; BRD = Bolivar Roads; GSC = Galveston Ship Channel; HSC = Houston Ship Channel; WE = West Bay. Time of day: 1 = morning; 2 = midday; 3 = afternoon.

surface salinity with a VISTA A366ATC refractometer and water temperature with a digital electronic thermometer, turbidity with a Sechii disk, and I used Beaufort scale as a sea state descriptor. In addition, I recorded the number of vessels and the number and family of seabirds within a 200 m radius using 1-minute scan sampling. Shrimp vessels within 200 m were also counted while on-effort.

Geospatial Analysis

Using Arcgis 9 tools (ESRI, 2004), I extracted bay water surface area from a digital map containing Galveston Bay (GLO[1]) and re-projected it into the UTM NAD_15N_1983 geographic coordinate system. By intersecting this map with a 500 m-cell grid (72x72 cells) (Fishnet, add-in Arcgis), I obtained the polygon layer on which the analysis was performed. In order to correctly align data to the grid, I used an aerial digital photography (TNRIS[2]) and GPS ground-truthed points. Each cell was labeled according to its location (Back Bay, Bolivar Roads, Galveston Ship Channel, Houston Ship Channel or West Bay) by intersecting the grid with five polygons corresponding to each section of the study area.

To optimally represent observed environmental conditions, surface maps of environmental variables measured during the surveys were obtained by Inverse Distance Weighted interpolation [3] computed by a VBA script applied to data obtained within the same time of day. Data points of dolphin counts and shrimp vessels were continuously recorded on effort and thus were not interpolated. When more than one measurement point was available per cell, the mean value was computed. To compute the distance from each cell to the main pass (Fig. 1), I built a distance layer using the CostDistance function in ArcGis 9 to calculate the shortest path by water from each cell grid to the Gulf of Mexico (GOM). I used 30 m-cell resolution for the raster output and then used

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[1] URL:<http://www.glo.state.tx.us/gisdata/gisdata.html>
[2] URL:<http://www.tnris.state.tx.us>
[3] $v = [\Sigma (1/d_i)^p v_i]/ \Sigma (1/d_i)^p$, where v – interpolated value
v_i – observed value
d_i - distance between observed and interpolated values
p – weighting coefficient

the tool "extract-values-to points" from Spatial Analyst to assign the distance from the raster to each grid cell. Depth was obtained from GEODAS 7.5 min x 7.5 min bathymetric maps with a 30 m-cell resolution (NOAA/NGDC[4]). I intersected a total of 184,703 soundings with our grid map to compute the mean depth of each grid cell.

To extract and calculate "on-effort" distances, a Perl script was developed to parse GPS survey tracks into "on-effort" sets of points as determined by stop/resume times in an Excel spreadsheet (Excel 2002, Microsoft). These were built into line segments using a VBA script and ArcObjects. I intersected the lines with the grid cells to determine the sampled cells. VBA and ArcObjects were used to integrate the data into a geo-referenced database. This raw matrix (n = 9,625) was then aggregated to the level of temperature season/salinity season/time of day/cell (n = 4,298) for the remaining analysis. Medians were used due to the skewed distribution of most of the variables.

Statistical Analysis

To describe the relationship between the response variable, dolphin presence, and environmental predictors (Table 2), I chose to use a Generalized Additive Model (GAM). The GAM is an extension of Generalized Linear Models (GLM) (McCullagh and Nelder 1989). The latter consist of regression techniques such as, log-linear and logistic that allow non-normal distributions of the response variable and more complex relationships between the response variable and explanatory variables than standard linear regression (Hastie and Tibshirani 1999, Dobson 2002). One advantage of GAMs over GLMs is the ability of GAMs to easily model nonlinear relationships between predictors and response (Hastie and Tibshirani 1999). This is especially relevant for the current analysis because of the large number of variables, their diverse nature (e.g., fixed variable such as depth and non-fixed variables such as turbidity, etc.) and wide range.

To model the relationship between the binary variable dolphin presence/absence I fitted the GAM, $\text{logit}(\mu)=\log[\mu/(1-\mu)]=\Sigma F_j+\Sigma s_i(x_i)$, where F_j are factors and $s_i(x_i)$ smooth (possibly linear) functions and μ is the probability of success (i.e., presence).

[4] URL: <http://www.hgdc.noaa.gov/mgg/geodas/geodas.html>

Model estimation was carried out in the statistical environment *R*[5], using the *mgcv* (Wood 2003, Wood 2004) package. The *mgcv* package fits a GAM by iteratively solving a penalized least squares problem then estimating the smoothing parameter by generalized cross validation (GCV). This procedure balances model fit against 'wiggliness' of the fitted functions (Wood and Augustin 2002).

All models were fit in the same manner: first a model was built using all environmental variables. The Deviance Explained and the GCV score were noted and used as criteria to

TABLE 2. Measurements of the environmental explanatory variables in the dataset. (n = 4,298).

Variables	Range	Minimum	Maximum	Mean	SD
Distance (km)	37.33	0.75	38.08	18.79	8.8742
Depth (m)	13.79	0.20	13.99	3.56	3.2212
Turbidity (m)	1.20	.10	1.30	.508	.1895
Salinity (ppt)	34.97	.03	35.00	19.13	5.6773
Water Temperature (°C)	24.06	8.59	32.65	22.99	6.4874
Shrimpers (#)	4.00	.00	4.00	.0417	.1943
Birds (#)	150.00	.00	150.00	9.367	15.021
Boats (#)	9.00	.00	9.00	.491	.7954

determine model fit. The p-value for each term in the regression was examined and the term with the highest p-value, i.e. the least significant, was discarded. The estimated degrees of freedom (edf) for each term were examined. If a term had an edf close to one it was converted to a linear term for the next version of the model. This process was repeated until all the remaining terms in the model were significant. Finally, to avoid overfitting the data, any term with more than 4 edf was forced to use at most 4 edf, and the model was fit a final time.

[5] URL: < http://www.R-project.org>

To investigate whether the same model adequately predicted presence of dolphins at the location level, I repeated the modeling process independently for the three locations that had a substantial number of sightings.

To test the null hypothesis that occurrence is independent from location, I performed a Pearson chi-square (X^2) on the contingency table and taking into account the total number of surveys (n = 367) by location. Because the null hypothesis was rejected, unplanned G_H test was performed to determine whether homogeneous subsets existed among locations (Sokal and Rohlf 1995).

For the temporal analysis, I considered a short-term variable (time of day) and two long-term variables that aggregated the months according to wet/dry and warm/cold patterns. The wet/dry seasons (i.e., salinity season) were defined by classifying months according to whether the estimated freshwater balance in Galveston Bay -- as computed by the Texas Water Development Board (TWDB[6]) -- fell above or below the annual mean calculated over a 9-year period (1992-2000). Likewise, warm and cold seasons (i.e. temperature season) corresponded to months in which water temperature rose above or fell below the annual mean calculated over a 5-year period (1996-2000) (NOAA[7], TCOON[8]).

RESULTS

Table 2 shows the environmental characteristics of the surveyed area as a whole. Preliminary assessment of the correlations among the variables showed correlations not strong enough to justify exclusion of terms.

In 2001, from January to December, 1,802 dolphins in 211 occurrences were detected in Galveston Bay (Fig. 2).

The test on independence of occurrence and location showed that occurrence of dolphins is not independent from location ($X^2_{[4]} = 98.85$, $p < 0.001$). Three groups were identified with distinct occurrences. These were in decreasing order: BRD/GSC;

[6] URL: <http://www.twdb.state.tx.us>
[7] URL:<http://co-ops.nos.noaa.gov/data_res.html>
[8] URL:<http:// lighthouse.tamucc.edu/pquery>

HSC/BB and WE. Fig. 3 displays the distribution of the sampling effort by location. Due to differences in area among surveyed locations, the sampling effort is uneven. Despite these differences, GSC, the location with the least total effort, belongs with BRD to the

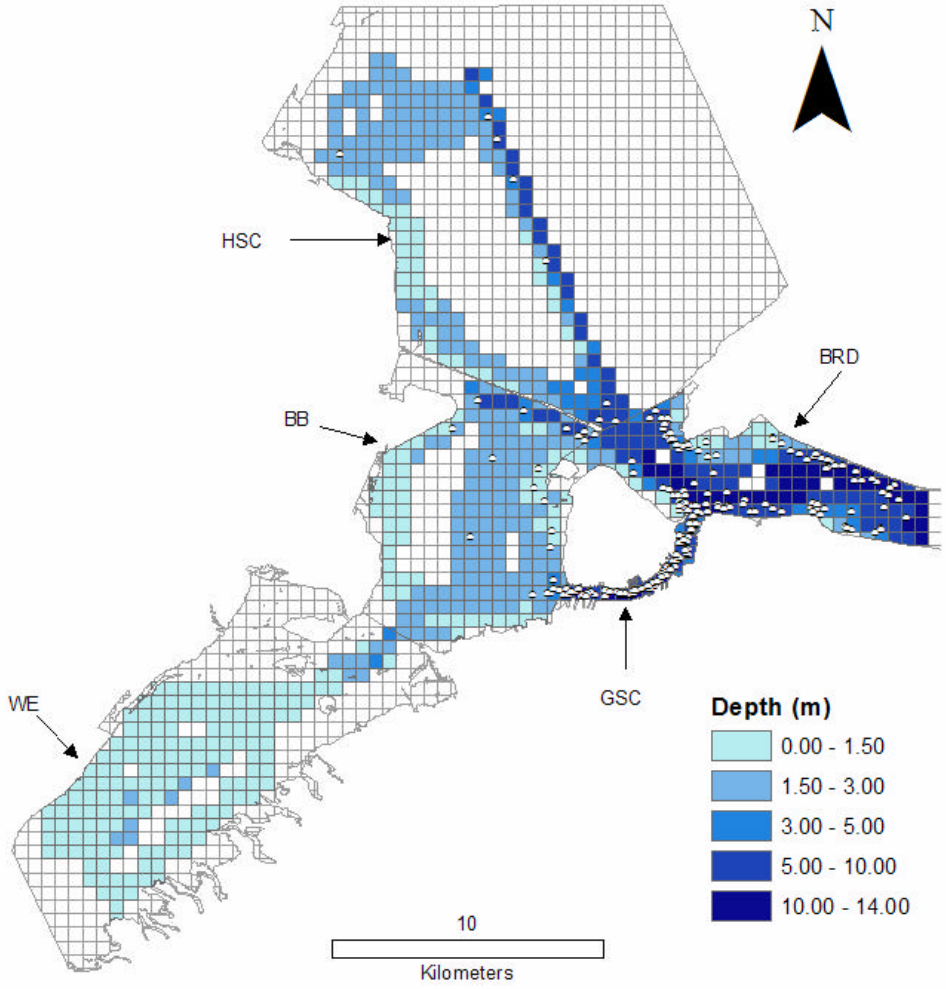

FIG. 2. Location of dolphin occurrences (circles) between January and December 2001. Bathymetry indicated in shades of blue. Blank cells show non-surveyed areas. (BB = Back Bay, BRD = Bolivar Roads, GSC = Galveston Ship Channel, HSC = Houston Ship Channel, WE = West Bay).

group with highest occurrence. BRD has the same level of effort as WE and is in the highest occurrence group, while WE is in the lowest occurrence group.

Deviance explained by the occurrence model for the entire bay was 32.6% of the total deviance (Table 3). As an attempt to obtain a simpler model, I excluded location, which resulted in a minor drop of the explained deviance (30.9%). I found that all the variables contributed significantly to predict dolphin occurrence (i.e. log odds of occurrence, hereafter referred as occurrence), except for temperature season, and turbidity, which were thus removed from the final model (Table 4a, b). The only linear term in the model was the median number of birds and median number of shrimpers.

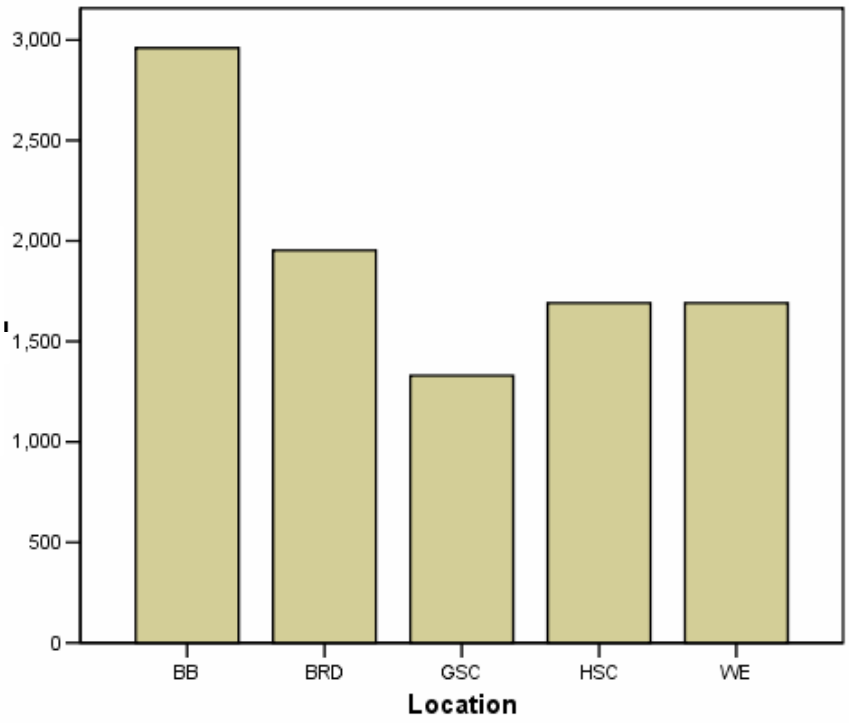

FIG. 3. Total effort by location. (total number of grid cells in raw matrix, n = 9,625). BB = Back Bay, BRD = Bolivar Roads, GSC = Galveston Ship Channel, HSC = Houston Ship Channel, WE = West Bay.

TABLE 3. Generalized Additive Models for the entire bay (with and without location as a term) and separately for each location (Back Bay, Galveston Ship Channel, Bolivar Roads). SH = Shrimpers, Sal_season = Salinity season, WaterTemp = Water temperature, GCV = Generalized Cross Validation.

Bay Location	Model	Deviance explained	R^2 adjusted	GCV score	n
Entire Bay with term Location (Formula A)	Occurrence ~ s(Salinity, k = 5) + s(WaterTemp) + s(Depth) + s(Boats, k = 5) + Birds + s(SH, k = 4) + s(Distance) + TimeDay + Sal_season + Location	32.6%	0.206	0.7874	4298
Entire Bay without term Location (Formula B)	Occurrence ~ s(Salinity, k = 5) + s(WaterTemp) + s(Depth) + s(Boats, k = 5) + Birds + SH + s(Distance) + Timeday + Sal_season	30.9%	0.189	0.8328	4298
Back Bay	Occurrence ~ s(Salinity) + SH + Distance	21.5%	0.141	1.1492	1157
Galveston Ship Channel	Occurrence ~ s(Boats) + s(Birds) + Depth + s(SH, k = 5)	18.9%	0.204	1.0991	319
Bolivar Roads	Occurrence~ s(WaterTemp) + s(Distance) + s(Boats, k = 5) + Birds + TimeDay + Depth	16.6%	0.125	0.9747	967

Note: k = knots, maximum estimated degrees of freedom (edf) ~ k-1

TABLE 4.a. Parameter estimates, standard error (SE), estimated degrees of freedom (edf) and significance level (*p*-value) for the Generalized Additive Model for the entire study area with location (Formula A).

	Estimated Coefficient	SE	edf	*p*-value
Parametric terms:				
(Intercept)	-4.5586	0.5394		$< 2.22 \times 10^{-16}$
Birds	0.0232	0.0036	1	1.32×10^{-10}
Midday	0.4938	0.1979	2	0.0126
Afternoon	-0.1402	0.2192		0.5224
Salinity season (wet)	0.4756	0.2412	1	0.0486
Location BRD	0.1327	0.4170	4	0.7504
Location GSC	0.9974	0.4034		0.0134
Location HSC	-0.8421	0.4437		0.0577
Location WE	-5.2419	2.8670		0.0676
Smooth terms:				
s(Salinity)			3.259	0.0169
s(Water Temperature)			5.204	4.251×10^{-8}
s(Depth)			4.658	2.356×10^{-5}
s(Boats)			3.599	0.0001
s(Shrimps)			2.783	0.0002
s(Distance)			4.355	2.851×10^{-5}

TABLE 4.b. Parameter estimates, standard error (SE), estimated degrees of freedom (edf) and significance level (*p*-value) for the Generalized Additive Model for the entire study area without location (Formula B). BRD = Bolivar Roads, GSC = Galveston Ship Channel, HSC = Houston Ship Channel, WE = West Bay.

	Estimated Coefficient	SE	edf	*p*-value
Parametric terms:				
(Intercept)	-5.4858	0.3423		$< 2.22 \times 10^{-16}$
Birds	0.0239	0.0035	1	2.03×10^{-11}
Shrimpers	1.3029	0.2577	1	4.44×10^{-7}
Midday	0.6540	0.2025	2	0.0012
Afternoon	0.0361	0.2202		0.8694
Salinity season (wet)	0.4990	0.2438	1	0.0407
Smooth terms:				
s(Salinity)			3.576	0.0124
s(Water Temperature)			5.007	3.48×10^{-6}
s(Depth)			1.870	2.77×10^{-8}
s(Boats)			3.668	2.33×10^{-5}
s(Distance)			4.181	$< 2.22 \times 10^{-16}$

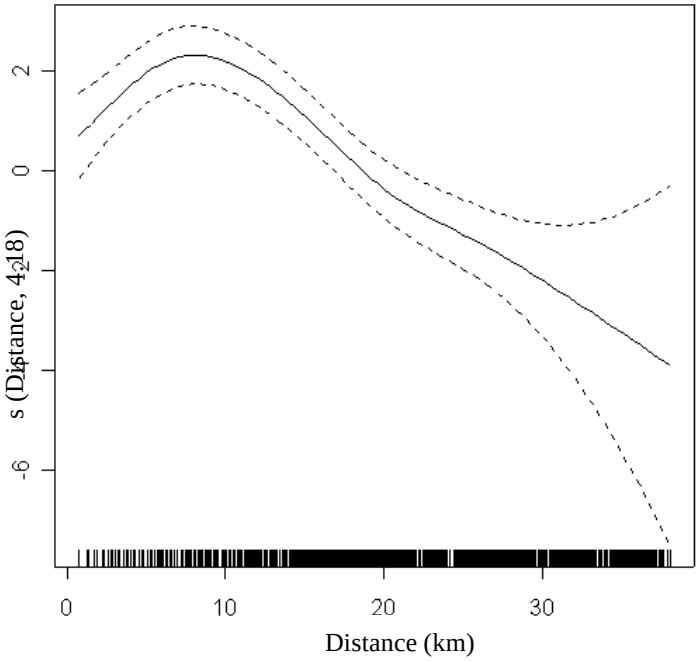

FIG. 4a. Smooth response curve for distance (km) to the Gulf of Mexico. All other variables are held constant to display the effect of salinity on the occurrence of dolphins. The ticks represent samples and broken lines represent the 95% Confidence Intervals.

The contribution of the smooth terms is represented in Figures 4a-e. Influence of a predictor increases as the values on the Y-axis depart from zero; above and below zero correspond to positive and negative influence, respectively. I found that the median distance reaches the highest absolute values, thus suggesting that it is the most influential predictor of the presence of dolphins. Caution is needed when interpreting the effect of distance (Fig. 4a) above 30 km due to the wide amplitude of the 95% confidence intervals. The maximum response, i.e., most common occurrence of dolphin sightings, occurred at 20º C (Fig. 4b), in approximately 14 m water depth (Fig. 4c) and at a distance of about 8 km from the Gulf waters (Fig. 4a). The influence of boats (Fig. 4d) is weaker than that of other elements and has the largest negative effect at an average number of one boat. Some reservation is needed in interpreting the influence of the median number of boats at the upper range; at this high point there is a scarcity of samples and there is considerable uncertainty as evidenced by the broad error

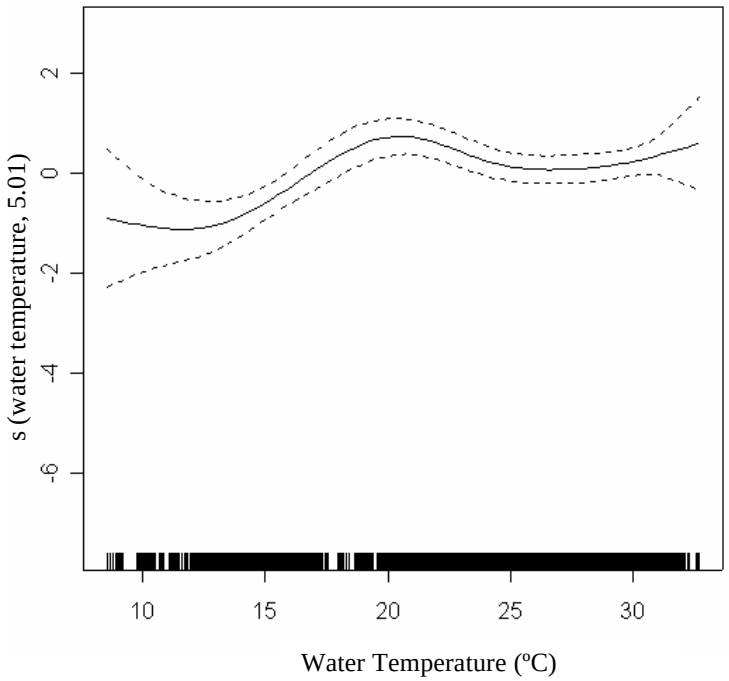

FIG. 4b. Smooth response curve for median surface water temperature (°C).

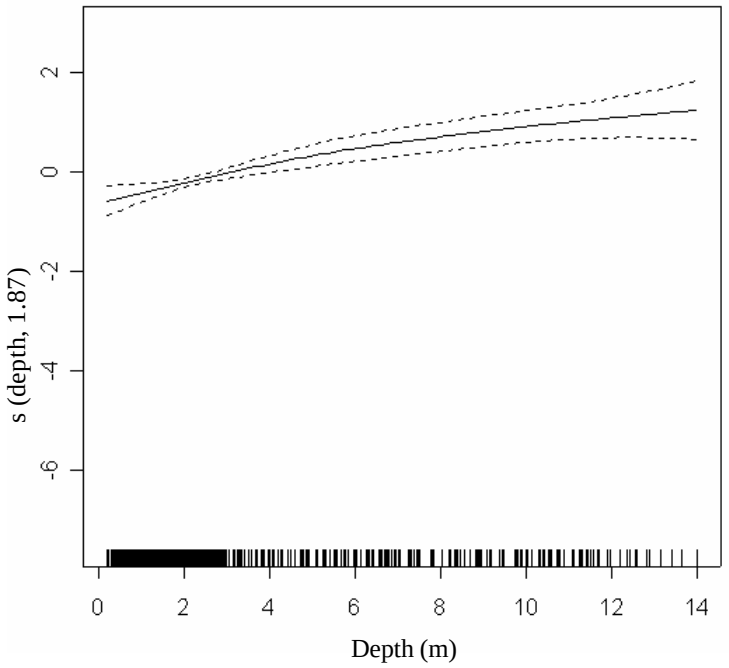

FIG. 4c. Smooth response curve for depth (m).

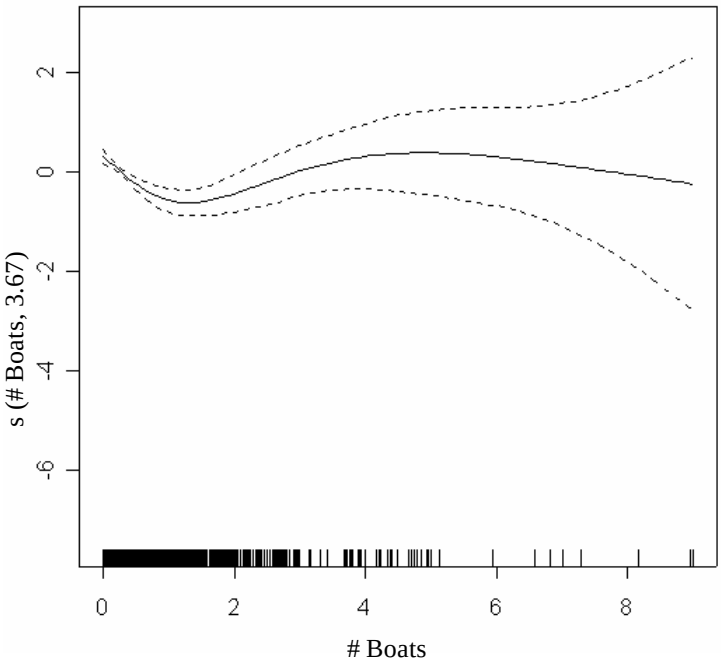

FIG. 4d. Smooth response curve for median number of boats.

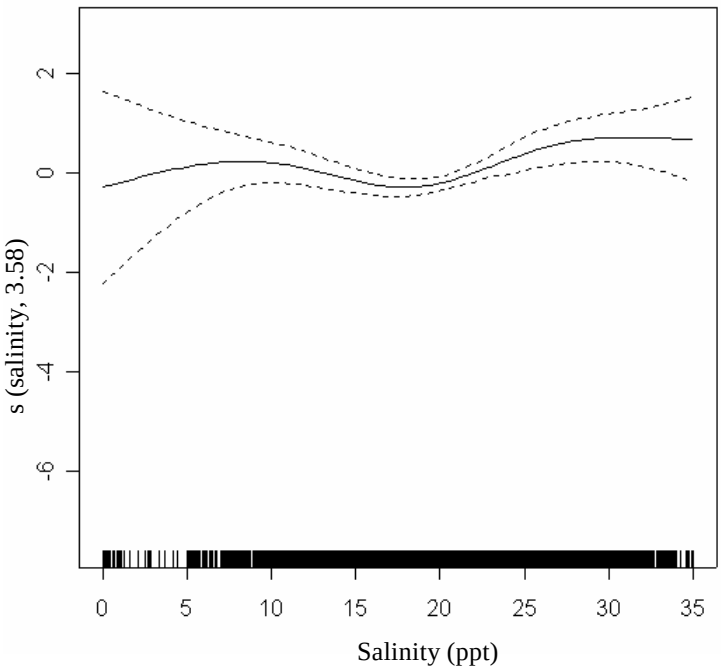

FIG. 4e. Smooth response curve for median surface salinity (ppt).

intervals. The response is negative until approximately 1.5 boats and has negligible impact above 3 boats. The influence of average salinity on the presence of dolphins is almost non-existent, showing a slight positive trend above 20 ppt and even smaller positive effect below 10 ppt (Fig. 4e). Fig. 5 depicts the combined influence of water temperature and salinity showing a larger response at higher water temperatures.

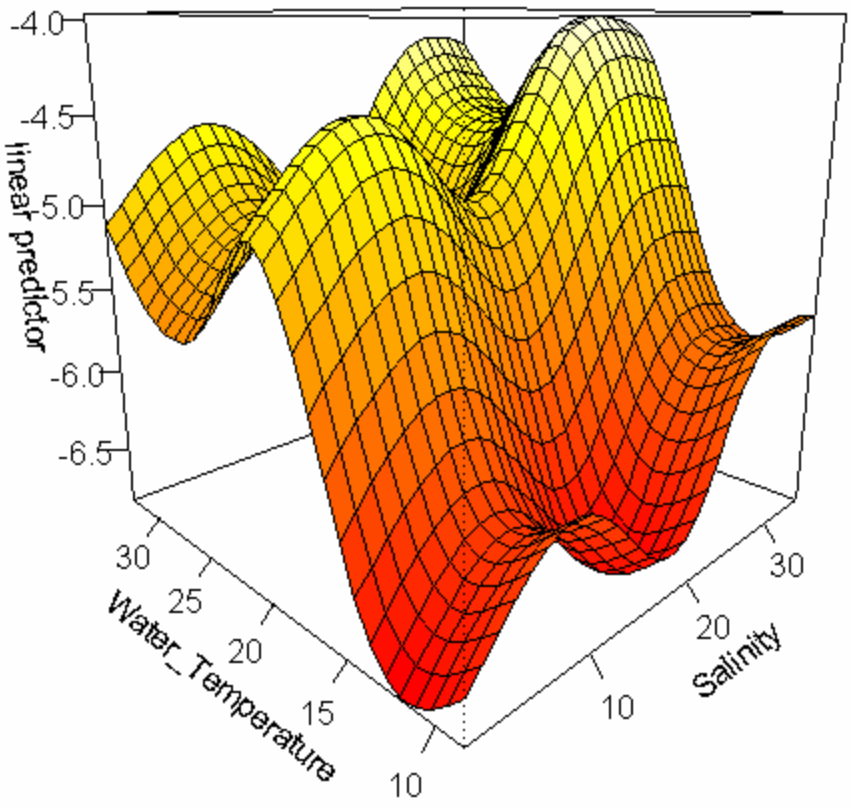

FIG. 5. Smooth response surface for median water temperature (°C) and median salinity (ppt) obtained with the overall model (without the factor location, i.e., Formula B). Linear predictor refers to log odds of occurrence. The color gradient represents the magnitude of the response (lighter represents a stronger effect).

Likewise, by plotting depth against distance (Fig. 6) we see that the response is mostly affected by distance, particularly at about 8 km. This distance, corresponding to a high occurrence of dolphins, is located in BRD and at the entry of GSC (Fig. 7).

Other highly significant elements positively associated with presence of dolphins were median number of birds and shrimp vessels, followed by time of day and the salinity season. As for time of day, mid-day had a stronger and positive influence compared to morning; afternoon, on the other hand, was not significantly different than morning.

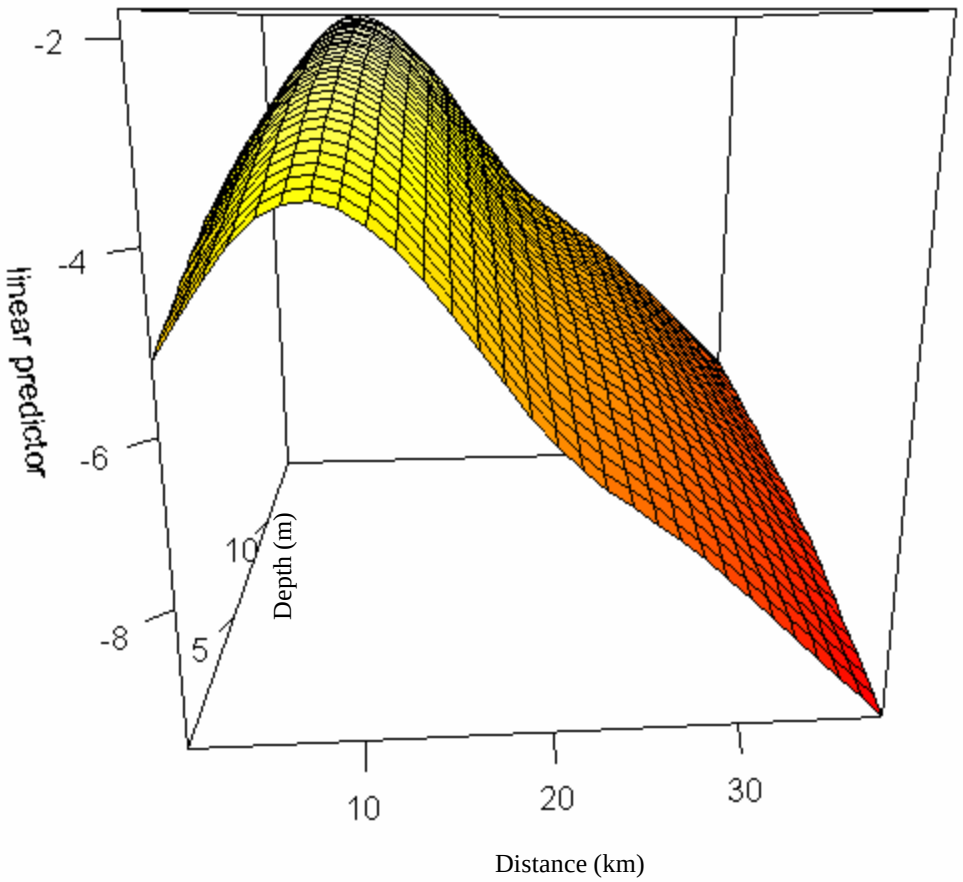

FIG. 6. Smooth response surface for distance to the Gulf of Mexico and depth obtained with the overall model (without the factor location, i.e., Formula B). Linear predictor refers to log odds of occurrence. The color gradient represents the magnitude of the response (lighter shades represent a stronger effect).

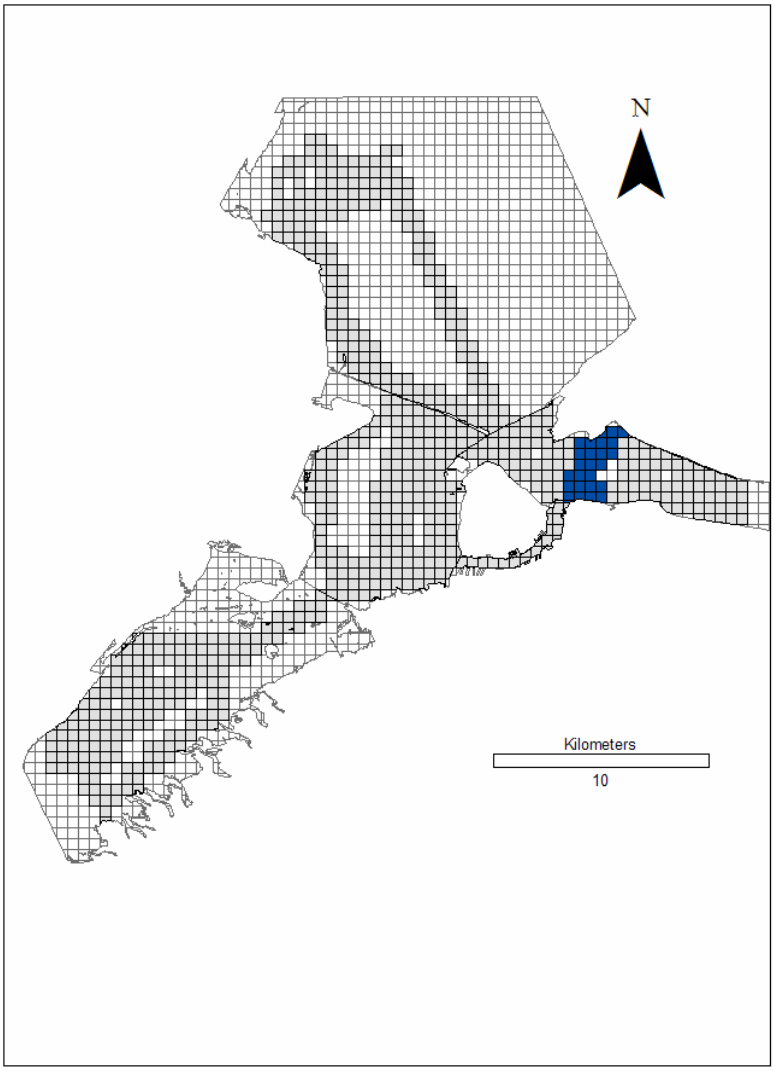

FIG. 7. Marked cells (dark blue) indicate 7 to 9 km distance from the Gulf of Mexico. Surveyed cells are shown in grey.

Salinity season, though barely significant, shows that sightings occur slightly more often in the wet (i.e., least saline) season, which corresponds to the months of February, May, July, August and November.

To graphically evaluate the performance of the model I mapped observations and predictions and compared the spatial patterns of occurrence (Fig. 8). For the chosen cutoff of 0.1 on probabilities and setting the factors at wet-warm seasons and midday, the map indicates a reasonable agreement in the general pattern: higher probability

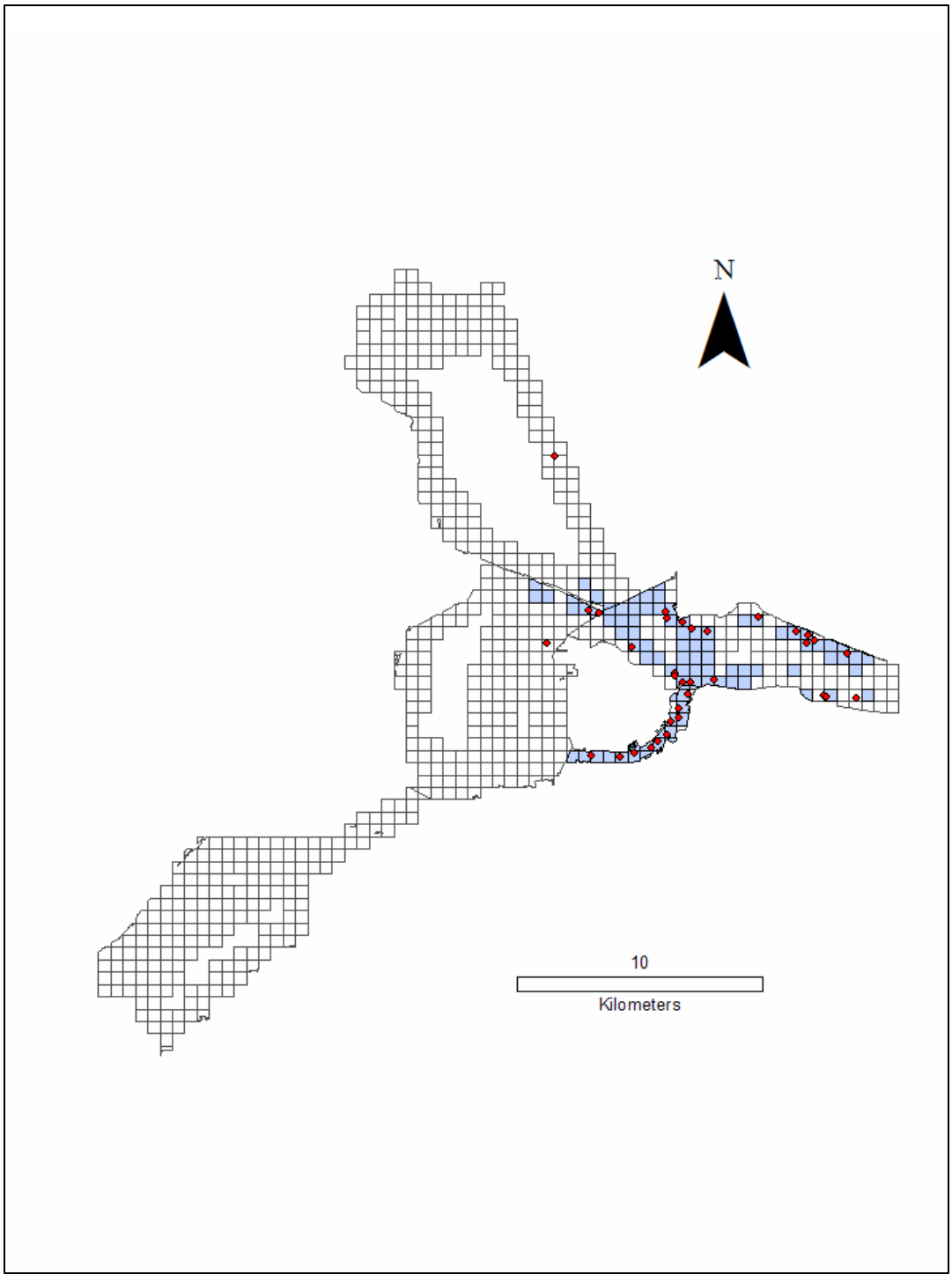

FIG. 8. Comparison of predicted occurrence (blank cells = no occurrence, blue shaded cells = occurrence) with observed occurrence (red dots) for midday during warm-wet seasons.

of occurrence in GSC and BRD. These two locations comprise only 21.49% of the total surveyed area and are responsible for 86.25% of the total sighted occurrences. Each occurrence may represent sightings of more than one group of dolphins. Hence, out of a total of 262 groups of dolphins observed, 88.93 % were distributed in these two locations. This concentration appears even more significant if we consider only the area of BRD and of GSC with sightings. In this case, 88.93 % of the groups were distributed in only 9.94% of the surveyed area.

Because of disparities among locations, I further examined the predictors separately for the locations with higher number of sighted occurrences (GSC, BRD) as well as for an intermediate location (BB). As expected, because of the different characteristics of these locations, the contributions of the predictors differed among locations (Table 3). The most noteworthy example is the influence of shrimp vessels, which appears to be important in GSC and BB but not in BRD. In GSC and BRD, both the number of birds and number of boats are important predictors. Moreover, time of day and water temperature influence the occurrence of dolphins in BRD but not in GSC.

DISCUSSION

Few studies have investigated the relative influence of both environmental and anthropogenic factors on bottlenose dolphin occurrence, and none, to my knowledge, have done so using fine temporal and spatial scales over a wide range of these variables. This study showed that even in a highly dynamic system such as the Galveston Bay (GB) estuary, certain variables are useful to predict bottlenose dolphin sightings and that these variables can differ at a small spatial scale, namely among locations ranging from 4 to 194 km^2.

Distance was an important predictor concurrent with the higher number of sighted occurrences in the two locations, Galveston Ship Channel and Bolivar Roads, closest to the Gulf of Mexico (GOM). Although at present the knowledge of site fidelity of this community (*sensu* Wells *et al*. 1999), or communities, is insufficient, we can confidently assume that a larger pool of bottlenose dolphins occurs in the GOM coastal waters

adjacent to the GB. Therefore, I would expect to find a higher occurrence of dolphins close to the GOM. This is, in fact, what I observed when I considered the five locations as a whole. However, I did not obtain a linear function of distance; and in Bolivar Roads, the closest location to the Gulf, the occurrence is highest at about 8 km from the Gulf. Thus, other factors must account for this skewed distribution further inside the bay.

Bolivar Roads lies between jetties and is the main passage for tidal exchange (GBEP 2002). It generates strong currents (Carillo and Berger 2001), and its waters are often characterized by salinity discontinuities (GBEP 2002). Bottlenose dolphins have been shown to associate preferentially with such tidal fronts, and it has been proposed that this behavior is related to feeding, as fish in such environments may either be aggregated or easier to capture (Mendes *et al*. 2002). In this study I did not examine the effects of tides, but it would be expected that if it were strictly a matter of tidal fronts then, as the front moved in and out during the tidal cycle, the dolphins would follow it and we would not observe this preferred site at 8 km from the Gulf. Further studies that take into account currents and tidal cycles, as well as behavior and movements (i.e., directionality) of dolphins in this location, are required to address this question.

The decrease in occurrences along the South-North axis can be associated with a decrease in salinity. This is supported by the occurrence of dolphins in the upper part of the bay (i.e., Houston Ship Channel) exclusively in the summer months (June-August) when mean salinity was 21.4 ppt. However, dolphins were also present in waters with very low salinity during and following a tropical storm ("Alison"), when salinity in most of the Galveston Bay was comparable to that of freshwater. The low salinity peak observed (Fig. 4e) may be attributable largely to the presence of dolphins despite the perturbing effect of this tropical storm. "Alison" occurred during the first ten days in June and this record-high precipitation for June (NOAA[9]) led to extremely low salinity (5 ppt) measured in the location closest to the Gulf.

It is also possible that the northern part of the HSC is a less favorable habitat in general for organisms due to higher levels of contaminants, including heavy metals

[9] URL:<http://www.srh.noaa.gov/hgx/projects/allison01>,
URL:<http://www.srh.noaa.gov/hgx/climate/iah/extremes/annualiah-top10.htm>

(GBEP 2002). Several areas of the HSC are subject to regular shellfish closures and in certain sites levels of contaminants above EPA standards and reduced oxygen levels have been detected (GBEP 2002). An alternative explanation for the South-North decrease in dolphin occurrence is the distribution of prey, whose size also decrease from the mouth to the head of the estuary (Patillo *et al*. 1995).

The dolphins' preference for deeper parts of the GB is evident even in those locations in which only a small portion of the total area consists of channels dredged to a depth of 10-13 m. For example, the average depth in the Back Bay and the Houston Ship Channel is about 2 m and most sightings in those locations were detected in the deeper channels. It is known that in deeper water fish species more susceptible to fluctuations of salinity and temperature seek refuge on the bottom of channels, where conditions are more stable (Patillo *et al*. 1995). Since bottlenose dolphins in estuaries and coastal waters feed primarily on benthic fish species (Barros and Odell 1990, Gannon and Waples 2004), they would benefit from this aggregation of fish at the bottom of the channels.

Galveston Bay is a wind-driven estuary; in open waters, strong winds, in particular from the North, can force the water to accumulate on one side of the bay while the opposite side becomes extremely shallow. Thus water levels can change rapidly, particularly during northerly winds in winter (GBEP 2002). There are several sand bars and places of depth less than one meter in the three shallowest locations, which are more prone to this wind effect because of their physiography. It is possible that under strong wind conditions parts of these locations become too shallow to be easily navigated by bottlenose dolphins. Indeed I have never observed bottlenose dolphins herding prey against the shore as they have been reported to do in other estuaries (Hoese 1971, Leatherwood 1975, Shane 1990).

The predictive influence of number of seabirds on dolphin sightings suggests that the occurrence of dolphins in the bay may be strongly related to distribution of their prey. The most common families of seabirds encountered were Laridae, Phalacrocoracidae and Pelicanidae. Species from these taxa feed primarily on fish (Bull and Farrand 1998). I observed that these seabird species feed regularly in close association with sighted

dolphins, including in proximity to shrimp boats. The diet of the bird species I observed may not closely overlap with the diet of bottlenose dolphins. For example, some bird species may target smaller fish than dolphins or may feed at the surface. However, even if seabirds target different fish species or sizes, these seabird prey species may attract larger fish species as predators, and these larger predators in turn may become prey to dolphins. BRD and GSC were the locations with the highest number of seabirds, which could hint at higher prey availability in these locations. However, these locations also offer more resting places for birds, and thus the presence of seabirds is not entirely related to feeding.

The positive correlation of sightings with shrimp vessels is not surprising. A previous study in Galveston Bay covering the GSC (Fertl 1994a) found that dolphins, including groups with calves, often feed in association with shrimp vessels. Commercial fishing is restricted in most of Bolivar Roads due to the intensive shipping and ferry traffic. Therefore, the number of shrimp vessels was not expected to be a contributor in the model of this location. Even though the data show a strong association of dolphins with shrimp vessels in the Back Bay, it remains unclear whether it is the presence of shrimp vessels that attract dolphins to this location. Most of the occurrences were detected on the boundaries of Back Bay with BRD and GSC. Thus, the presence of dolphins in the Back Bay could be a “spill over” effect due to proximity to the above high occurrence areas.

The weak effect of high densities of boats seems to indicate that bottlenose dolphins can remain in very busy waters, assuming that these areas present otherwise favorable conditions. Groups with calves and neonates were commonly encountered in the locations with the most intensive vessel traffic. This does not necessarily imply that vessel traffic has no negative impact on dolphins. Many of the dolphins identified photographically bear scars, some of which may well have been inflicted by boat collisions. Several studies focusing on the influence of boat traffic on bottlenose dolphins have shown short-term responses of dolphins to boats (e.g., Hastie *et al*. 2003). In Sarasota Bay, Florida, changes in swimming behavior occurred mostly in shallow

waters and the authors suggested that this may be related to a greater difficulty to locate the position of the approaching vessel due to decreased sound propagation compared to deeper waters (Nowacek *et al*. 2001). On the other hand, bottlenose dolphins off the Sein Island, Brittany also use a harbor as a resting area (Liret 2001).

I found that the effect of boats appears stronger and more negative when only a few vessels are present. This may imply that dolphins cope less well with irregular and unpredictable traffic, and that they avoid areas with such conditions. Other studies on vessel traffic impact on estuarine bottlenose dolphins (Wells 1993, Allen and Read 2000) indicated that dolphins temporarily avoided certain areas when, on weekend days, the traffic increased. However, even though the intensity of recreational traffic in those areas is likely similar to that in Galveston Bay, the latter has a much larger number of types of vessels such as ferries, tankers, and their support vessels. These larger vessels are more predictable in their paths than are recreational boats, and the larger vessels are often favored by dolphins for bow-riding. Detailed studies on the response of dolphins to vessel traffic in the Galveston Bay are needed to fully address why dolphins here appear to cope well with high-intensity vessel traffic. Boats and seabirds have a highly variable spatial distribution, and it is possible that interpolation may have led to an oversimplification and that a more frequent sampling scheme would more adequately reflect the conditions concurrent with dolphin sightings. This problem is not raised for the number of shrimp vessels, however, because these boats were recorded continuously and simultaneously with dolphin counts.

The finest temporal scale in this study, time of day, had a significant influence on the sightings of dolphins. If a large proportion of the dolphins encountered use both the bay and the coastal waters, this may reflect an influx of dolphins in the morning. This explanation is also supported by the higher number of dolphins observed close to the Gulf (BRD) in the mornings and increasingly sighted further into the bay towards the afternoon. Although our knowledge about bottlenose dolphin nocturnal behavior is scarce, in most areas they appear to be more active in daytime than at night (Reynolds *et al*. 2000). I speculate that a larger number of dolphins are in the bay during morning and

mid-day hours primarily to feed. However, some behaviors such as resting are less conspicuous; if they occur more often in the morning or afternoon, this phenomenon could result in underestimation of sightings at these hours. Furthermore, dolphins may have sought more protected sites outside our study area as resting or socializing areas.

Time of day was an important predictor in Bolivar Roads but not in GSC, indicating a more uniform temporal distribution of dolphins in GSC compared to BRD. This could be attributed to a sampling bias or, alternatively, to other factors such as the lure of shrimp vessels that may mask or dilute the effect on sightings of time of day. Commercial fishing occurs throughout the day, except from mid-April to mid-August, when a closure in the afternoon is imposed for shrimp catches. Even if this closure results in a decrease in active shrimp boats in the GSC and a decrease of dolphins in the afternoon, this diminution likely would not be sufficiently pronounced to cause a radical shift in the predictive influence of time of day over the entire year since the shrimp boats operate for the preponderance of the year (seasonal closures after 2:00 pm from mid-April to mid-August).

The overall seasonal effect was moderate in the case of salinity seasons and undetected for temperature seasons. This finding contrasts with the strongest water temperature effect relative to salinity. It is possible that it is a result of the correlation between salinity/salinity seasons and water temperature/temperature seasons. A more plausible explanation, however, is that both water temperature and salinity, in contrast to the seasons, are more valid markers of the conditions that the dolphins experienced. Salinity, meanwhile, is known to influence the distribution of estuarine species. This prompted the characterization of salinity seasons for Gulf of Mexico estuaries (Orlando *et al*. 1993). According to this model, four seasons can be distinguished in Galveston bay: low (April-June), increasing (July), high (August-October) and decreasing (November-March). I refrained from using this model, however, because if I had done so, the tropical storm conditions of 2001 would not have been captured. The alternative of using a 9-year annual estimated freshwater balance that accounts for inputs and losses of freshwater in the bay allowed us to compare the characteristics of 2001 to this long-

term mean. It proved to be a predictive indicator for the overall area but not at the level of certain locations.

In GSC, surface water temperature and surface salinity also did not appear to be important predictors of dolphin sightings, whereas the influence of those factors differed between BRD and BB. Water temperature appeared meaningful in BRD and salinity seemed significant in BB. Since BRD is close to the Gulf, salinity is unlikely to suffer as much fluctuation as in the BB, where circulation was substantially reduced by the construction of an 8.5 km dike (GBEP 2002).

The influential role of water temperature on the occurrence of dolphins, overall and in BRD, with at least one local maximum at about 20° C, indicates that the warmer conditions are more favorable to a larger number of dolphins, possibly migratory individuals or periodic residents, who are more likely to remain in BRD, the closest location to the Gulf. A similar relationship of dolphin abundance to water temperature was found in inshore and coastal waters of Virginia Beach (Barco *et al*. 1999). According to Barco *et al*. (1999), movements out of bay and coastal waters when the water temperature dropped below 16°C, appeared to show a lower limit of their thermoneutral zone. In parts of their range, bottlenose dolphins migrate from high to low latitudes during winter (Kenney 1990). On the other hand, year-round residents of Sarasota, Florida show tolerance to seasonal temperature fluctuations (Scott *et al*. 1990). Whether the higher occurrence at approximately 20° C in this study reflects physiological, social or reproductive needs or is associated with movements of their prey remains to be investigated. I suggest that year-round resident dolphins, estimated at 200 individuals in previous studies (Bräger 1993), most regularly frequent GSC, where anthropogenic factors are useful to predict their presence. Influxes of dolphins from the Gulf or other estuaries, particularly during higher water temperatures, lead to a higher number of dolphins in BRD, and even to dispersion further north into the HSC. This phenomenon is consistent with findings from other estuaries along the lower Texas coast (Shane 1980), in which the trend is reversed, i.e. higher abundance of dolphins in the

winter, and could explain the source of the dolphins migrating into Galveston Bay. Analysis of site fidelity patterns will be pursued in future studies.

CONCLUSIONS

The presence of dolphins may not reflect a preference for the environmental conditions as a whole but may instead represent a trade-off among different ecological requirements. The models obtained for the presence of bottlenose dolphins may not coincide with those predicting abundance, which when combined with the behavioral component can give further insight on habitat use.

In the Galveston Bay, bottlenose dolphins are more likely to occur in certain locations, and the most influential factors were highlighted in this study. I showed that, as common in ecological studies, the responses of bottlenose dolphins to most of the factors analyzed were non-linear. I suggest that similar approaches that: (1) allow for non-linear responses; (2) select a set of predictor variables as comprehensive as possible and that cover a range representative of the study area, and (3) use a fine spatial and temporal scale, may be particularly useful to understand determinants of coastal dolphin occurrence, especially in estuaries, and may help to generate hypotheses about habitat use.

In addition, I provide needed baseline information for the conservation of this species in GB, which was classified as an estuary of national significance by the EPA (USEPA, 1999). Specific measures for the conservation of bottlenose dolphins have not yet been implemented in the 1995 Galveston Bay Plan that is still effective at this date (GBNEP 1995). In 2001, 6,613 vessels used the Port of Houston[10] and 890 vessels used the Port of Galveston[11]. Considering the intensity of current or planned shipping activity, in particular related to liquefied natural gas and crude oil, and in view of the overlap of shipping channels with the most favorable bottlenose dolphin habitat, it is deemed important that emergency plans incorporate measures to minimize the impact of oil spills

[10] URL:<http://www.portofhouston.com/busdev/tradestatistics.html>
[11] URL:<http://www.portofgalveston.com/news/stats.shtm>

in this habitat and to contemplate specific measures to rescue potentially affected dolphins (see, for example, Smultea and Würsig 1995). Dredging, at least in the short term, may also be an important source of disturbance for dolphins -- directly, by physically restricting access to certain areas, or indirectly, due to re-suspension of pollution-contaminated sediments. This study and similar methodologies may help policy makers determine the most appropriate periods for dredging and other construction/habitat change activities.

CHAPTER III

ENVIRONMENTAL PREDICTORS OF BOTTLENOSE DOLPHIN CORE FEEDING DENSITIES IN THE GALVESTON BAY, TEXAS

SYNOPSIS

Estuaries are productive inshore systems that serve as important nursery grounds, including for bottlenose dolphins. Several hydrographic features such as bathymetry, salinity, and turbidity influence prey distribution. Shrimp vessels also aggregate prey. Galveston Bay offers a useful model to evaluate factors that determine bottlenose dolphin feeding habitat: presence of dolphins year-round; occurrence of feeding tactics with and without shrimp vessels; strong anthropogenic influences by shrimp fisheries, shipping, and tourist boating; and diverse physiographic conditions.

From January to December, 2001, I conducted monthly boat surveys in five locations of Galveston Bay totaling 3,814.77 km of search effort. A total of 1,802 dolphins in 262 groups were detected, 56.87% of which were feeding. Dolphins feeding exclusively in association with shrimp vessels comprised 21.48% of feeding groups. The most common group size in the 500 m-wide Galveston Ship Channel (GSC) was two dolphins, contrasting with six in the open waters of Bolivar Roads (BRD). These two locations amounted to one-fifth of the surveyed area, but accounted for 94% of all feeding groups.

By the use of a 500 m-resolution grid on seasonal and time of day time scales, I associated dolphin counts, behavior and group size with environmental variables collected at fixed stations and after group-follows, including water temperature, salinity, turbidity, number of boats and birds. I used a Generalized Linear Model to evaluate the association of these environmental variables -- as well as distance to coastal waters and depth -- with density in feeding cores (i.e. core feeding densities, CFDs). The strongest effect was distance to the Gulf, which was inversely correlated with density. Interestingly, CFD was positively correlated with number of boats.

Using geospatial analysis, I identified prime feeding habitats and found that the main CFDs were stable with time of day and season. These CFDs were situated in channels,

on ferry landings and close to a break in the jetties. This fine-scale study of bottlenose dolphin distribution may contribute to a better understanding of habitat requirements for coastal dolphins, particularly in estuaries with intensive human activities.

INTRODUCTION

Foraging behavior profoundly influences many aspects of an organism's ecology, including habitat use, movement patterns and social organization. The interaction with social organization is particularly evident among mammals. The foraging plasticity of bottlenose dolphins (*Tursiops truncatus*) has been well documented: for example, changes in group size may occur intra-specifically as dolphins shift from individual foraging in coastal waters to group foraging offshore (Würsig 1986). This change in foraging tactics is explained based on optimal foraging theory, which postulates that efficient foragers minimize cost/benefit when searching, chasing and handling their prey (Smith 1978). Hence, the observed differences in dolphin group sizes are thought to result from different costs associated with patterns of prey distribution: more clumped, high density and unpredictable prey schools tend to favor formation of larger dolphin group sizes, whereas dispersed and non-schooling fish in coastal environments favor smaller group sizes (Norris and Dohl 1980).

Based on the foraging phase that involves the largest energy expenditure, animals may be viewed as either “searchers” or “pursuers” (Pianka 1994). The former spend most of their energy searching for their prey, whereas “pursuers” spend more energy chasing and capturing their prey. Consequently, “searchers” tend to be generalists and “pursuers” more selective hunters of their quarry (Pianka 1994). The same categorical scheme may be applied to bottlenose dolphins. Given that the distribution of their prey appears to be patchy and highly variable, they would seem likely to fall into the class called “searchers.” In fact, like searchers, bottlenose dolphins are generalists, feeding on a variety of pelagic and benthic taxa, which include fish, cephalopods and crustaceans (Shane *et al*. 1986, Barros & Odell 1990). It is reasonable to expect that those dolphins able to use environmental cues to identify prime feeding habitat are more efficient

foragers and thus have enhanced survival compared to those dolphins unable to do so. In other words, the ability to find prime feeding habitat appears likely to constitute a major natural selection pressure in a highly dynamic environment.

Estuaries are highly productive marine nursery areas and typically have a complex habitat structure that promotes a diverse and sometimes erratic distribution of organisms, creating a dynamic habitat mosaic of poor to good feeding conditions (Alongi 1998, McLusky and Elliot 2004, Örnólfsdóttir *et al*. 2004). Although the bottlenose dolphin is arguably the best studied delphinid, knowledge of its habitat selection and how it may adjust its behavior to environmental changes is limited even in the case of more accessible inshore environments. This paucity of data stems from difficulties inherent in studying foraging in marine species under natural conditions, such as the complexity of characterizing habitat conditions and the discontinuity in observing feeding behavior (Alonso *et al*. 1995). Few studies are available that describe the environmental conditions that enhance feeding habitat for bottlenose dolphins. Foraging studies of bottlenose dolphins in estuaries have shown that they feed in association with tidal fronts, which tend to be high-productivity zones (Mendes *et al*. 2002). Bottlenose dolphins in Sarasota Bay show preference for seagrass habitat, which constitutes a refuge and feeding area for many fish species. Bottlenose dolphins seem to adapt their foraging behavior rapidly to anthropogenic changes, for example by feeding in association with fishing boats (Leatherwood 1975, Norris and Dohl 1980, Shane *et al*. 1986, Fertl 1994a).

Bottlenose dolphins are common in the Galveston Bay estuary (GB), Texas. Since 1990, several studies (e.g. Bräger 1993, Maze & Würsig 1999) have been conducted on distribution and behavior of the dolphins in this area. More than 1,000 individuals have been identified in the GB and environs and it has been estimated that about 200 are permanent residents (Bräger 1993).

Seagrass habitat is in rapid decline in GB (GBEP 2002), and thus is unlikely to offer sufficient resources to sustain the large numbers of dolphin observed in this area. However, human activities such as shrimp fishing boats and apparent disturbance of prey

by commercial shipping may present alternative feeding opportunities for bottlenose dolphins.

The goals of this study are to: (1) identify primary feeding habitat for bottlenose dolphins in GB; (2) investigate whether high feeding density areas (i.e. CFDs) occur in this highly dynamic environment, and if so, to examine their spatial stability across two different time scales; (3) evaluate which environmental factors -- natural and anthropogenic -- are associated with CFDs; (4) determine group size during foraging and examine the influence of environmental conditions on group size, and (5) estimate the relative importance of feeding in association with shrimp vessels.

METHODS

Study Area and Data Collection

The study area is located in the Galveston Bay estuary (29°30' N, 94°40' W), the second largest estuary on the Texas coast (NOAA 1990). As is typical of most Gulf of Mexico estuaries (Nelson and Monaco 2000), GB contains three salinity zones: tidal fresh (<0.5ppt), mixing zone (0.5-25ppt), and seawater zone (>25ppt). Galveston Bay is a shallow estuary (average 2 m) with mud and sand flats and dredged channels of up to 15 m maintained for navigation. In addition to shipping, commercial and recreational fisheries are an important human use of the bay. The Lower Galveston Bay survey area, comprised of a total area of 170 km^2, was divided into five sections (Fig. 1) to capture different natural and anthropogenic environmental conditions.

I conducted 367 surveys in 5 m and 5.7 m outboard vessels over 124 days from January 22, 2001 to December 29, 2001, for a total of 3,814.77 km of search distance. A survey refers to a given combination of date/location/time of day. If weather conditions allowed, each location was surveyed at least once a month in morning, midday and afternoon periods. Time-of-day categories were formed by dividing daylight hours into 3-intervals. Survey tracks consisted of pre-defined routes traveled at an average speed of 14 km/hr. Positions were stored in a Garmin 48 GPS at 1-minute intervals for subsequent estimation of effort and mapping of dolphins and environmental data.

Once a group of dolphins was detected, the search effort ceased. Number of dolphins and calves was estimated, and group behavior was classified using scan sampling and instantaneous recording (Martin and Bateson 1993) for five minutes. A dolphin group was defined as all dolphins within 100 m of their nearest neighbor (adapted from Wells *et al*. 1987). Behaviors were classified as traveling, socializing, feeding, feeding with shrimp vessels (following beside or behind the boat or the nets or swimming near a stationary boat), resting, and unknown (adapted from Shane 1990, Hanson and Defran 1993). More than one behavior may occur in the same group. Because feeding behavior is the focus of this study, I classified traveling, socializing and resting as "other" and considered any group where feeding occurred as "feeding." Mixed groups refer to those where both "feeding" and "other" occurred.

In order to maintain constant detectability of dolphins, I implemented the following measures: 1) surveys were carried out only at or below sea state 3 (Beaufort scale); 2) one observer covered 90 degrees from the bow to the right and a second observer covered 90 degrees to the left; 3) groups detected while following another group or while collecting environmental data were excluded; and 4) groups detected beyond 200 m from the survey position were excluded *a posteriori* using a buffer in ArcGis 9 (ESRI 2004).

I collected environmental data at 22 fixed stations and after a group scan, when the group was located more than 500 m from a station or after more than one hour had elapsed following the previous measurement. Surface salinity was measured with a VISTA A366ATC refractometer and water temperature with a digital electronic thermometer, turbidity with a Sechii disk, and Beaufort scale was used as a sea state descriptor. In addition, I recorded the number of vessels and seabirds within a 200 m radius using 1-minute scan sampling. Shrimp vessels within 200 m of the trackline were counted on-effort.

For the seasonal analysis, I used temperature and salinity seasons. The wet/dry seasons (i.e., salinity season) were defined by classifying months according to whether the estimated freshwater balance in Galveston Bay -- as computed by the Texas Water

Development Board (TWDB[12]) -- fell above or below the annual mean calculated over a 9-year period (1992-2000). Likewise, warm and cold seasons (i.e. temperature season) corresponded to months in which water temperature rose above or fell below the annual mean calculated over a 5-year period (1996-2000) (NOAA[13], TCOON[14]).

Geospatial Analysis

Using geospatial tools (Arcgis 9), I built a 500-m cell grid (Fishnet 1998), which was intersected with a digital polygon map of the Gulf of Mexico (GLO[15]) to obtain the water surface area of interest. The environmental dataset, dolphin counts, behavior and effort data were stored in a geodatabase and projected onto the grid using the UTM NAD_15N_1983 geographic coordinate system.

To optimally represent observed environmental conditions, surface maps of environmental variables measured during the surveys were constructed by Inverse Distance Weighted interpolation[16] of data gathered during the same time of day. Data points of dolphin counts and shrimp vessels were continuously recorded on effort and thus were not interpolated. When more than one measurement point was available per cell, the mean value was computed.

In addition to the environmental data collected, I calculated mean depth and distance to the main pass to the Gulf of Mexico (Fig. 1) for each cell. Depth was obtained from GEODAS 7.5 min x 7.5 min bathymetric maps with a 30 m-cell resolution (NOAA/NGDC[17]). I intersected 184,703 soundings with the grid map to compute the mean depth of each cell. To compute the distance, I built a distance layer using the CostDistance function in ArcGis 9 to calculate the shortest path by water from each cell grid to the GOM. I used 30 m-cell resolution for the raster output and then used the tool

[12] URL:<http://www.twdb.state.tx.us>
[13] URL:<http://co-ops.nos.noaa.gov/data_res.html>
[14] URL:<http://lighthouse.tamucc.edu/pquery>
[15] URL:<http://www.glo.state.tx.us/gisdata/gisdata.html>
[16] $v = [\Sigma (1/d_i)^p v_i] / \Sigma (1/d_i)^p$, where v – interpolated value
v_i – observed value
d_i - distance between observed and interpolated values
p – weighting power
[17] URL<http://www.hgdc.noaa.gov/mgg/geodas/geodas.html>

"extract-values-to-points" from Spatial Analyst to assign the distance from the raster to each grid cell.

To extract and calculate "on-effort" distances, a Perl script was used to parse GPS survey tracks into "on-effort" sets of points as determined by stop/resume times. These sets were built into line segments, which were intersected with the grid cells and integrated with the other datasets in the geo-referenced database using VBA and ArcObjects. Each record contains the number of times that a given cell was sampled to standardize the number of dolphins and shrimp vessels by effort. I define mean encounter rate as the number of dolphins per cell corrected by the number of times that the cell was sampled.

To calculate behavior proportions and group size, a matrix stratified by date/time of day/cell was used. This matrix was then aggregated to the level of month/time of day/cell for the remaining analysis. Medians were used due to the skewed distribution of most of the variables. I refer to "occurrence" as a data point that represents 1-2 groups of dolphins encountered in the same month/time of day/cell. Of the total occurrences, only six cases resulted from combining multiple groups.

Kernel densities were calculated on the mean encounter rate with a 10-meter raster resolution and 1 km search radius. I performed separate kernel density analysis for all occurrences and for subsets of seasons (warm and cold) and time of day (morning, midday, and afternoon). I defined "core feeding densities" (CFD) as the region with densities at or above 2 standard deviations from the mean. For the CFD analysis I selected only the occurrences (n = 85) within the CFD zone and, using the "extract-value-to-point" tool, assigned the corresponding density value (mean encounter rate/km^2).

To determine whether feeding occurrences showed a spatial pattern or were randomly distributed, I used the Global Moran's I function on the mean encounter rate using Euclidean distance. A Moran's I value near +1.0 indicates clustering; a value near –1.0 indicates dispersion and the z-score value indicates if it is statistically significant (ESRI, 2004).

To evaluate the level of clustering of high and low mean encounter rate, I used the Getis-Ord General G Index. A high/low index value indicates that high/low values are clustered within the study area and z-scores indicate whether the index value is statistically significant (ESRI, 2004).

To compare the location of the mean center of all the CFDs in different seasons and times of day, I obtained the mean center based on Euclidean distance and weighted by feeding density. All geospatial analyses were performed using the Spatial Analyst and Spatial Statistics toolboxes in Arcgis.

Statistical Analysis

To test the null hypotheses that group size is the same in GSC and BRD, I used the median test, a distribution-free procedure, which is suitable for small samples and assumes that all samples have the same shape but the outcome is little affected when shapes are not quite the same (Zar 1996). Median tests were also used to compare environmental conditions in CFDs to environmental conditions in the overall study area, as well as in the main feeding locations (GSC and BRD) when no dolphins were sighted. The latter tests were bootstrapped 1,000 (on overall area subset) and 2,000 times (on GSC/BRD subset) on random sub-samples (n = 100) of environmental conditions when no dolphins were sighted. To test the null hypothesis that feeding density was the same among CFDs, the non-parametric Kruskal-Wallis test was used.

To determine whether the environmental and temporal variables could be accommodated as predictors of feeding density, I fitted a General Linear Model (GLM) Univariate procedure (McCullagh and Nelder, 1989) with a Gaussian error distribution and the identity link function. I used Type II sums of squares to test main effects. Following the law of parsimony (Occam's Razor), a simpler or more parsimonious model has advantages. With a less parsimonious model, the unexplained variability decreases (Dobson 2002) and the significance values of other sources of variation may become inflated. In addition, considering the sample size and number of explanatory variables, only main effects were tested. Density was entered as the response variable

and salinity season (dry: February, May, July, August and November; wet: all other months), temperature season (warm: April to November; cold: all other months) and time of day were entered as fixed factors. All other environmental variables were entered as covariates. The Levene test was used to check for homoscedasticity of residuals. Analysis of residuals led to the log-transformation of density and to the exclusion of two cases with undue influence on the estimation of regression coefficients. A GLM was refitted on the sample without those outliers (McCullagh and Nelder 1989). To assess if observations collected sequentially were independent, I plotted the residuals following the same sequence. No pattern was revealed, thus dependency was not suspected.

Selection of a parsimonious model was performed by evaluation of the Akaike Information Criteria (AIC) (Read and Cressie 1988) and adjusted R^2 (Zar 1996). The AIC is a function of the log-likelihood corrected for the number of model parameters (-2 maximized log-likelihood + 2 # parameters in the model). Smaller values imply a better model fit (Read and Cressie 1988).

The coefficient of determination (R^2) estimates the proportion of the total variability in Y (dependent variable) that can be explained by the dependence of Y on all independent variables in the regression model (Zar 1996). To compare models with distinct number of independent variables, the adjusted coefficient of determination is an adequate test to the goodness of fit. In addition, R^2 adjusted is a better estimate of the population coefficient of determination (Zar 1996).

All statistical analyses were performed with the *SPSS* 12.0 and *R* 2.0.1 packages.

RESULTS

In 2001, from January to December, 1,802 dolphins were detected in 262 groups. Feeding was the most commonly observed behavior, representing 56.87 % of the total groups and 66.52 % of identified behaviors (Fig. 9). Of the feeding behaviors 33.56% consisted of mixed behavior groups. Thus, most groups were exclusively feeding, amounting to a total of 632 dolphins. Feeding in association with shrimp vessels combined with other behaviors (FSH, FSHPLUS, FFSH, FFSHPLUS) occurred in

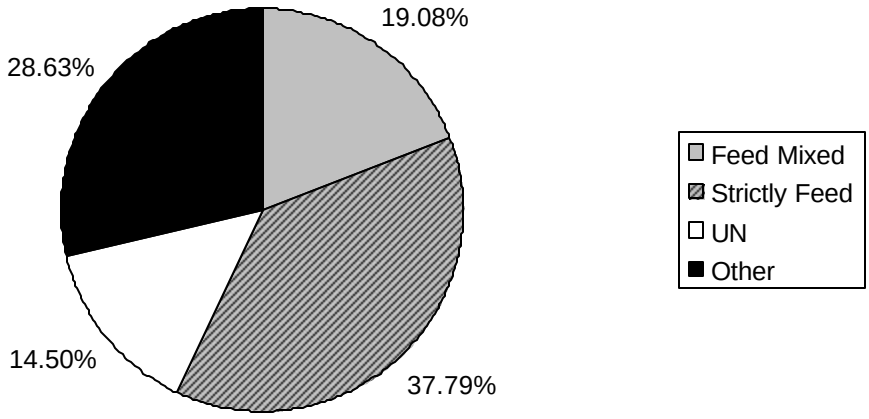

FIG. 9. Percentage of behaviors for dolphin groups (n = 262). Feed Mixed = feeding and other behavior in the same group, Strictly Feed = only feeding in the same group, UN = undetermined, Other = not feeding. Feeding is comprised of Feed Mixed and Strictly Feed.

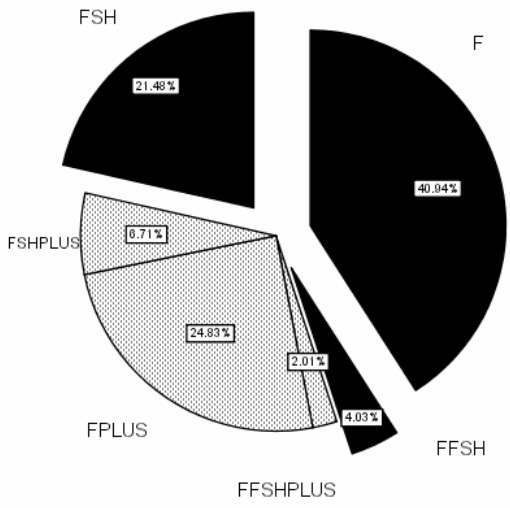

FIG. 10. Percentage of feeding behaviors in 262 groups of dolphins. Expanded slices (black) strictly feeding and stippled slices feeding mixed with other behaviors. (F- feeding without shrimpers; FSH – feeding in association with shrimpers; PLUS – non-feeding behaviors).

34.23% of the feeding groups, and 21.48% of the groups were feeding exclusively in association with shrimp vessels, a total of 204 dolphins (Fig. 10).

The median feeding group size was six, even when excluding feeding groups with mixed behaviors (Table 5). Group size was significantly ($p<0.001$) smaller in GSC (median = 4) than in BRD (median = 7) ($X^2_{[1]} = 16.119$, $p <0.001$). In GSC, the mode was 2 dolphins per group, and in BRD, it was three-times higher.

Of a total of 149 feeding groups (Fig. 11), 135 were found in GSC (n = 76) and BRD (n = 59), which correspond to 0.06 and 0.03 groups per sampled cell, respectively (Fig. 12). These two locations comprise only about one-fifth (21.49%) of the entire area surveyed, yet accounted for 94% of the feeding groups. The feeding encounter rate in BRD (mean = 7.30, S.E. = 0.83) was more than two times higher than in GSC (mean = 3.02, S.E. = 0.35) (Table 6).

TABLE 5. Group size in Bolivar Roads (BRD), Galveston Ship Channel (GSC) and all locations with mixed feeding groups (F+FMIX) and excluding mixed feeding groups (F-FMIX).

	BRD	GSC	F+FMIX	F-FMIX
N valid	59	76	149	99
Mean	9.034	5.632	6.899	6.384
Standard Error	.741	.474	.41399	.499
Median	7.000	4.000	6.000	6.000
Mode	6.000	2.000	6.000	2.000†
Minimum	1.000	1.000	1.000	1.000
Maximum	30.000	19.000	30.000	30.000
Percentiles				
25	6.000	2.000	3.000	2.000
50	7.000	4.000	6.000	6.000
75	12.000	8.000	8.000	8.000

† multiples modes exist. The smallest value is shown.

TABLE 6. Mean encounter rate in Bolivar Roads (BRD) and Galveston Ship Channel (GSC).

Location	N	Mean	Median	Std. Error	Minimum	Maximum
BRD	57	7.3041	5.0000	.83343	.50	30.00
GSC	72	3.0211	2.0000	.34719	.20	15.00

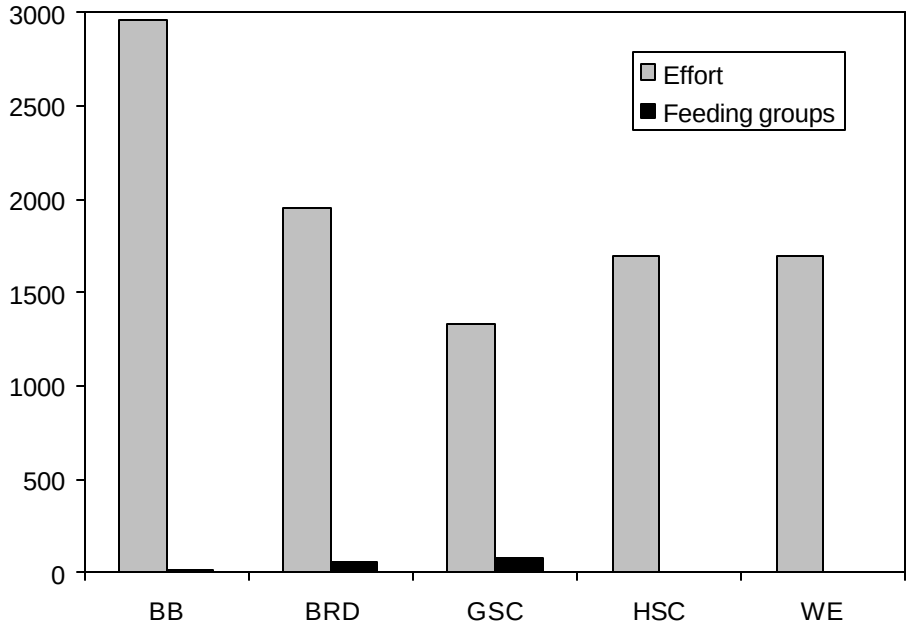

FIG. 11. Effort (total number of cells sampled) and number of feeding groups by location. (BB = Back Bay; BRD = Bolivar Roads; GSC = Galveston Ship Channel; HSC = Houston Ship Channel; WE = West Bay).

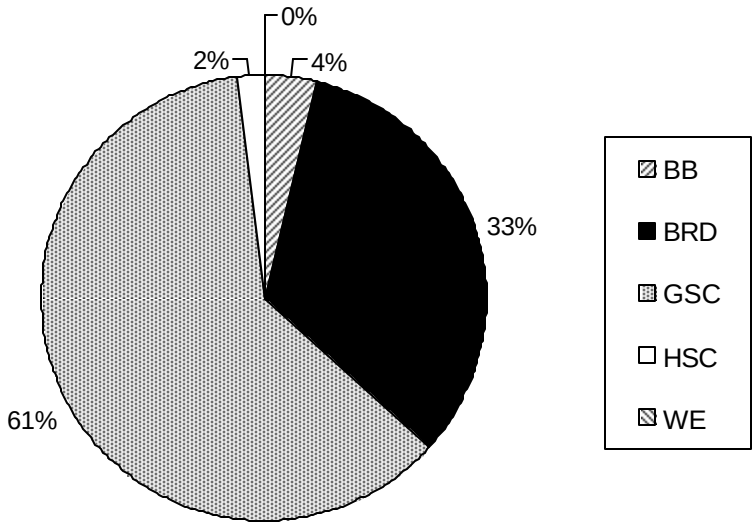

FIG. 12. Percentage of feeding groups (number of feeding groups/total number of sampled cells) by location. (BB = Back Bay; BRD = Bolivar Roads; GSC = Galveston Ship Channel; HSC = Houston Ship Channel; WE = West Bay).

The distribution of feeding events exhibited a highly clustered pattern with a less than 1% likelihood of occurring by chance (Moran's Index = 0.14, z = 5.5 S.D.). In terms of the overall feeding distribution, the low encounter-rate clusters exhibited a higher degree of aggregation than did the high encounter-rate clusters (General G Index = 0.084, z = -2 S.D.).

Fig. 13 shows the overall feeding density clustered into six CFDs. Density differed among CFDs ($H = 35.08$, $p<0.001$). The main CFDs were BRD8 and GSC3, where density surpassed 3 SD (above 42.86 mean encounter rate/km^2), followed by BRD4 and GSC2. The lowest density CFDs were BRD10 and GSC1. The most persistent across seasons and time of day was GSC3, followed by BRD8 and BRD10. The weighted mean center of core feeding zones shifted slightly with temperature season and time of day. In the cold season (Fig. 14a), the mean center was located inside the Galveston Ship Channel, and in the warm season (Fig. 14b) the mean center was situated in Bolivar Roads. Similarly, the mean center was positioned in the GSC in the morning (Fig. 15a) and in BRD from midday (Fig. 15b) to afternoon (Fig. 15c).

When all factors and environmental predictors were included, the predictive model of CFD (i.e. equal or above 2 SD) explained more than half of the density variation (R^2= 60.7%). Of a total of 11 variables (Table 7), 5 were significant predictors: distance ($p<0.001$); boats ($p<0.001$); depth ($p< 0.01$); water temperature ($p< 0.01$) and temperature season ($p< 0.01$). The final model (Table 8) with only the latter five variables, decreased R^2 to 55.0% but resulted in only a moderate decrease in R^2 – adjusted (53.9% to 52%) and the AIC improved (-59.84 to -62.74). Therefore, we chose this more parsimonious model.

Density was inversely correlated with distance and water temperature and positively correlated with number of boats and depth. Higher density was predicted during the warm than in the cold season. Given the same conditions for the predictors, the expected log-density in the warm season would be approximately 0.19 higher than in the cold season.

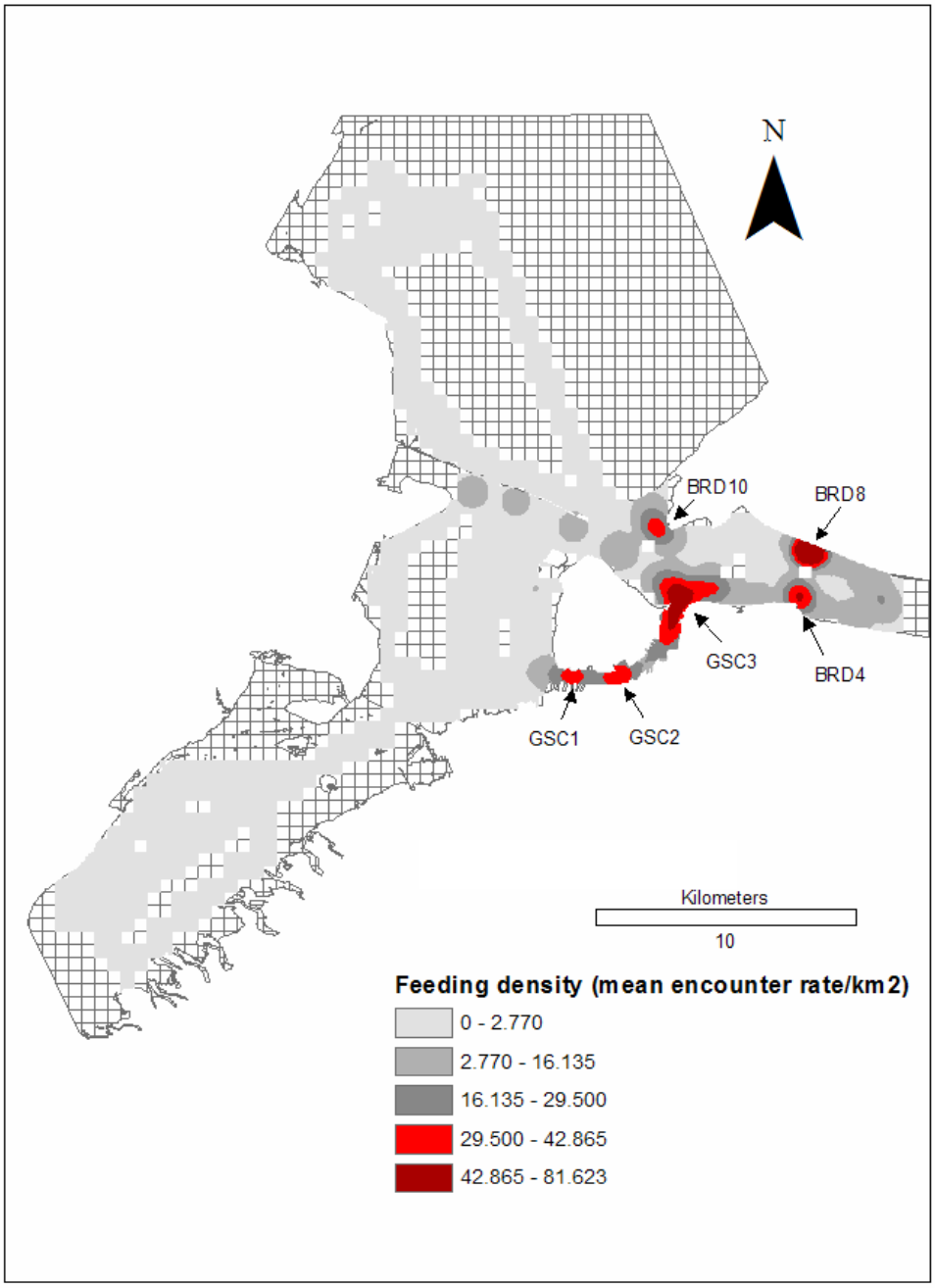

FIG. 13. – Location of core feeding densities (shown in red 2 SD = [29.50, 42.86[; 3 SD = [42.86, 81.62]).

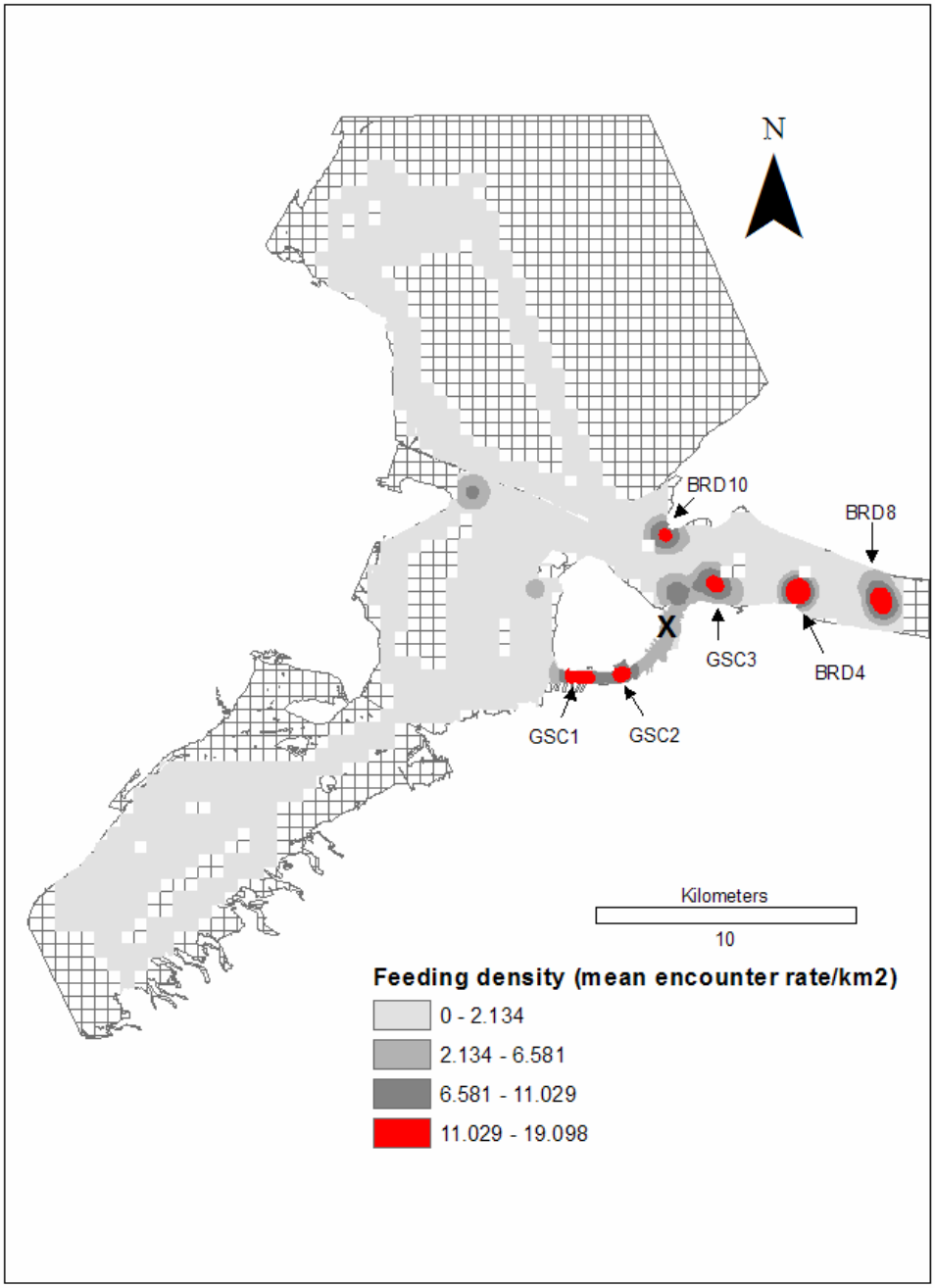

FIG. 14a. Location of core feeding densities (in red) during the cold season. X indicates mean weighted center. (2 SD = [11.03, 19.10[ ).

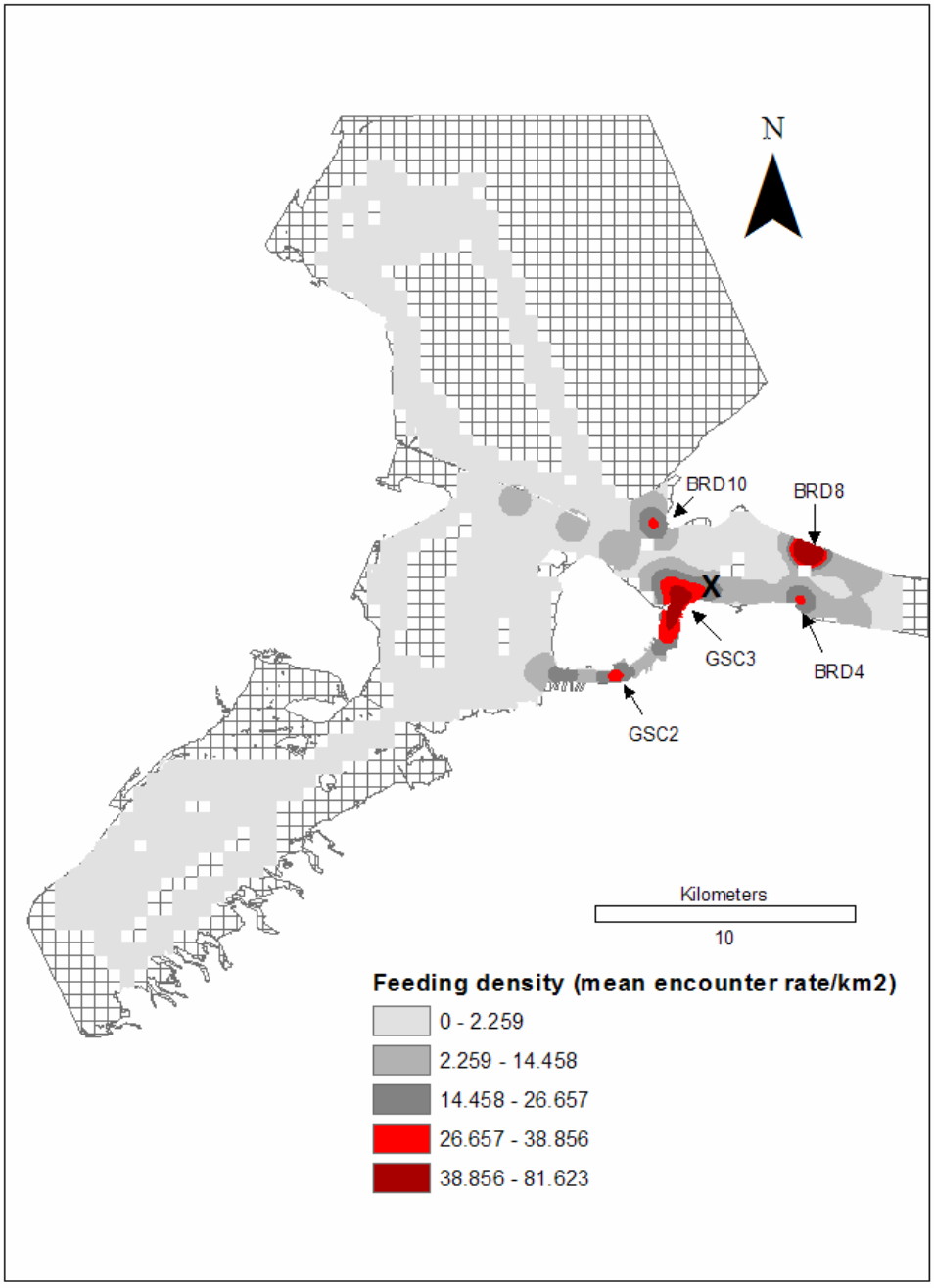

FIG. 14b. – Location of core feeding densities (in red) during the warm season. X indicates mean weighted center. (2 SD = [26.66, 38.86[, 3 SD = [38.86, 81.62]).

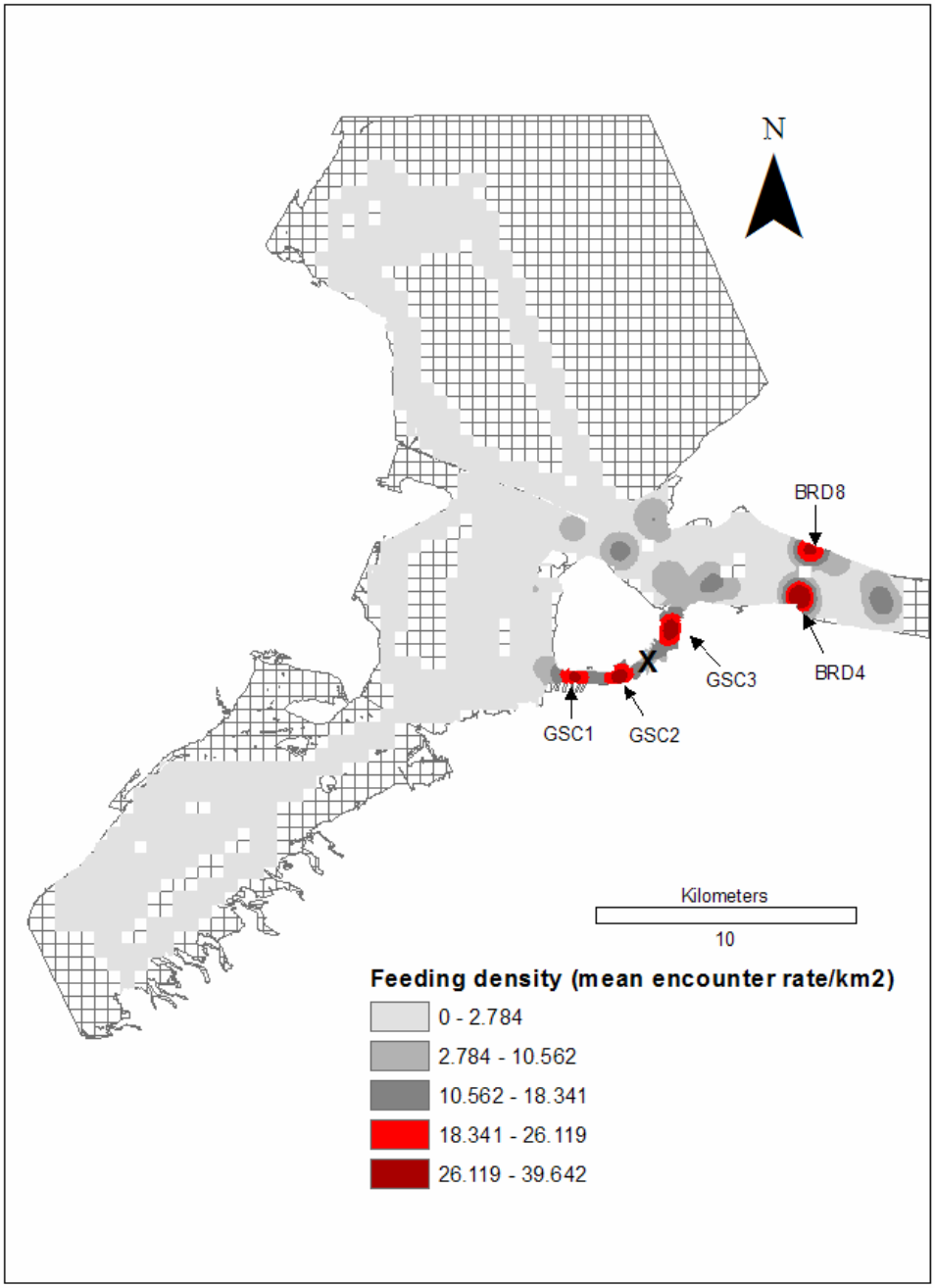

FIG. 15a. Location of core feeding densities in the morning. X indicates mean weighted center. (shown in red 2 SD = [18.34, 26.12[, 3 SD = [26.12, 39.64]).

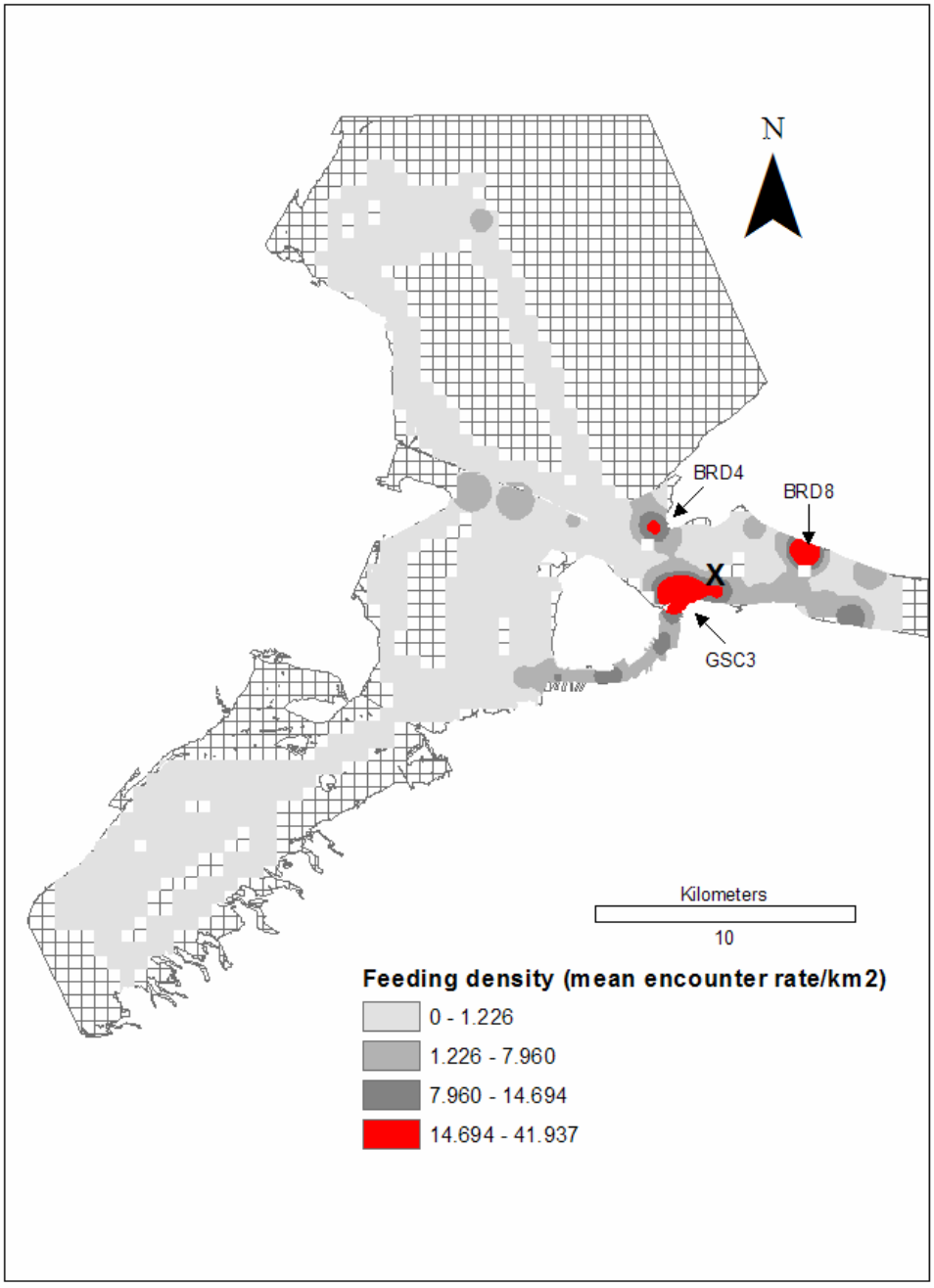

FIG. 15b. Location of core feeding densities in the midday. X indicates mean weighted center. (shown in red 2 SD = [14.70, 41.94]).

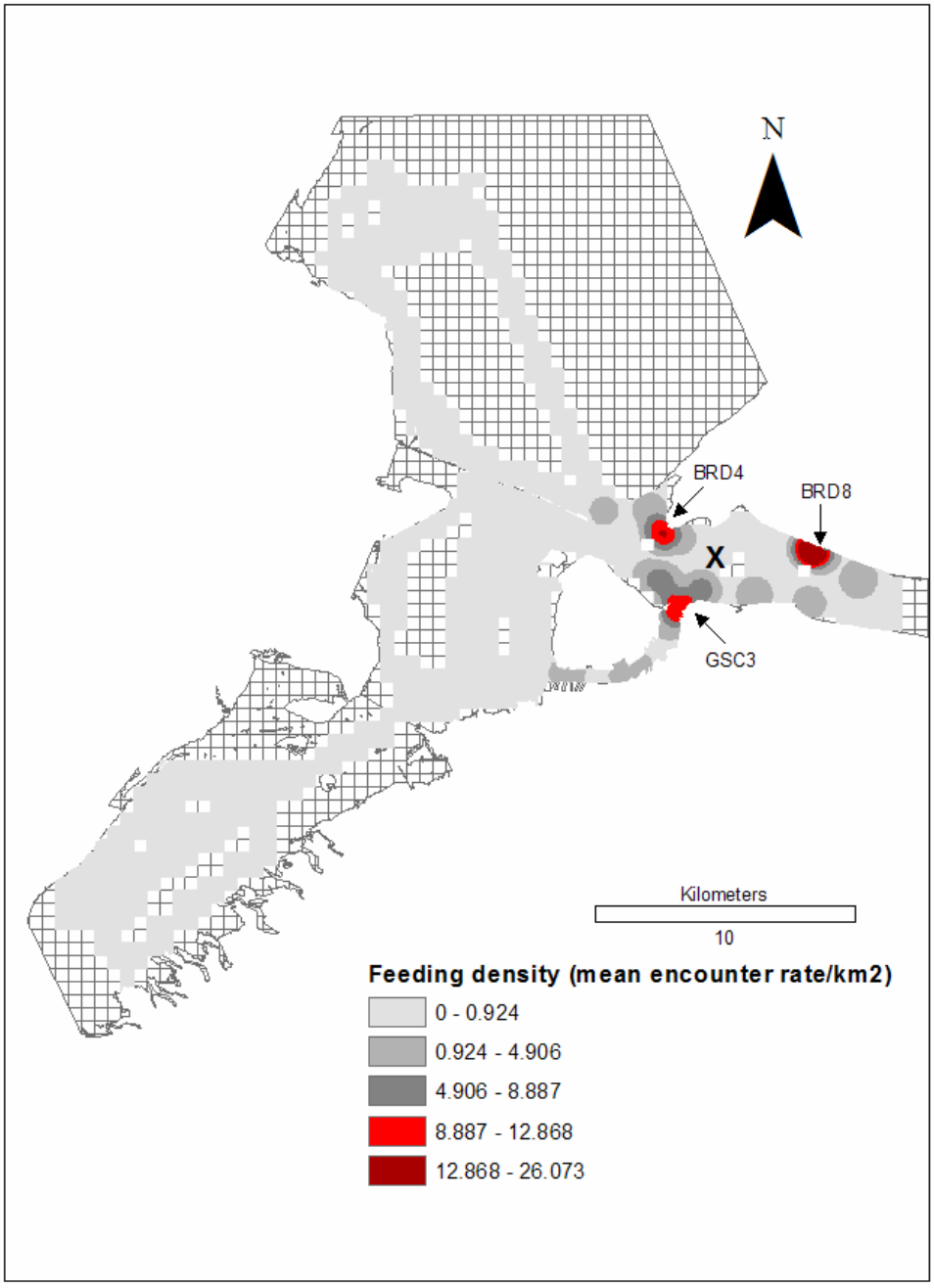

FIG. 15c. – Location of core feeding densities in the afternoon. X indicates mean weighted center. (shown in red 2 SD = [8.89, 12.87[, 3 SD = [12.87, 26.07]).

TABLE 7. Full model (GLM) fitted to the log-transformed core feeding density. LN (Density)= Turbidity + Salinity + Water temperature + Boats + Birds + Shrimpers + Salinity_season +Temperature_season + Time_day + Distance + Depth. (Adjusted R Squared = 0.539; AIC : -59.843)

Explanatory variables	Estimated Coefficients	SE	*P*
(Intercept)	3.962	0.204	$< 2 \times 10^{-16}$ ***
Turbidity (m)	0.131	0.120	0.279
Salinity (ppt)	0.001	0.004	0.735
Water_temperature (ºC)	-0.014	0.005	0.006 **
Boats	0.042	0.012	0.001**
Birds	-0.0006	0.0006	0.263
Shrimpers	0.047	0.044	0.284
Salinity_season (wet)	0.078	0.059	0.191
Temperature_season (warm)	0.196	0.068	0.006 **
Time_midday	0.077	0.044	0.084
Time_afternoon	0.094	0.055	0.092
Distance (km)	-0.050	0.007	6.39×10^{-10} ***
Depth (m)	0.023	0.007	0.002 **

* P < 0.05; ** P < 0.01; *** P < 0.001.

TABLE 8. Reduced model (GLM) fitted to the log-transformed core feeding density. LN (Density)= Water temperature + Boats + Temperature_season + Distance + Depth. (Adjusted R Squared = 0.521; AIC : -62.74)

Coefficients	Estimate	SE	Partial Eta Squared	*P*
(Intercept)	4.264	0.120	0.942	$< 2 \times 10^{-16}$ ***
Water_temperature (ºC)	-0.016	0.005	0.125	0.0014 **
Boats	0.028	0.010	0.094	0.0061 **
Temperature_season (warm)	0.186	0.068	0.090	0.0074 **
Distance (km)	-0.054	0.006	0.487	8.91×10^{-13} ***
Depth (m)	0.021	0.007	0.118	0.0019 **

* P < 0.05; ** P < 0.01; *** P < 0.001.

Of the statistically significant terms, distance has by far the greatest effect on feeding density followed, in decreasing order of relevance by water temperature, depth, boats and temperature season.

Except for turbidity and water temperature, environmental conditions in the CFD zone and the conditions in the entire study area when no dolphins were detected differed significantly (Tables 9a, b). In general, feeding cores were deeper and closer to the Gulf and exhibited higher salinity, number of boats, birds and shrimp vessels.

When compared only to the area of GSC and BRD when dolphins were not sighted, the feeding cores were deeper and tended to show higher numbers of birds. Other tested environmental predictors (distance, water temperature, turbidity, salinity, number of boats and number of shrimp vessels) were not significantly different (Tables 10a, b).

TABLE 9a. Frequency below and above the median of environmental predictors in the entire bay (GB) when no dolphins were sighted compared to feeding cores - one example from the bootstrapping procedure (1000 repetitions).

Environmental Predictors	GB zero dolphins		Feeding Cores	
	<= Median	> Median	<= Median	> Median
Depth	73	27	17	66
Distance	26	74	66	17
Turbidity	56	44	36	47
Salinity	61	39	31	52
Water Temperature	52	48	40	43
Birds	76	24	16	67
Boats	68	32	24	59
Shrimpers	99	1	70	13

TABLE 9 b. Test statistics from the Median test comparing environmental predictors in the entire bay when no dolphins were sighted with feeding cores - one example from the bootstrapping procedure (1000 repetitions).

	Depth (m)	Distance (m)	Turbidity (m)	Salinity (ppt)	Water Temp. (°C)	Birds	Boats	Shimpers (#/cell)
N	183	183	183	183	183	183	183	183
Median	-5.5748	12769.6094	.5073	20.5041	24.5000	8.0134	.4978	.0000
Chi-Square	50.052	51.964	2.892	10.148	.263	58.374	27.714	13.802
Df	1	1	1	1	1	1	1	1
P	.000	.000	.089	.001	.608	.000	.000	.000
Yates' Continuity Correction								
Chi-Square	47.973	49.845	2.409	9.224	.133	56.127	26.173	11.805
df	1	1	1	1	1	1	1	1
P	.000	.000	.121	.002	.716	.000	.000	.001

TABLE 10 a. Frequency below and above the median of environmental predictors in the Galveston Ship Channel (GSC) and Bolivar Roads (BRD) when no dolphins were sighted compared to feeding cores - one example from the bootstrapping procedure (2000 repetitions).

Environmental Predictors	BRD – GSC zero dolphins		Feeding Cores	
	<= Median	> Median	<= Median	> Median
Depth	59	41	29	54
Distance	52	48	42	41
Turbidity	58	42	35	48
Salinity	47	53	45	38
Water Temperature	49	51	43	40
Birds	58	42	34	49
Boats	56	44	36	47
Shrimpers	92	8	70	13

DISCUSSION

Feeding is a major diurnal activity for bottlenose dolphins in the Galveston Bay estuary (GB). This is unsurprising considering the role of estuaries as nurseries for organisms in general (Alongi 1998, McLusky and Elliot 2004). Although comparison with studies that quantified activity of bottlenose dolphins is difficult because of differences in methodology, particularly discontinuities in classifying behavior, these results appear to agree with others conducted in estuaries. I found that feeding accounted for over 55 % of the behavior. Similarly, in the western most part of Galveston Bay, feeding was reported as the most common behavior (Maze 1997). Bräger (1993) analyzed frequency of behaviors and reported that the incidence of feeding behavior

TABLE 10 b. Test statistics from the Median test comparing environmental predictors in the Galveston Ship Channel (GSC) and Bolivar Roads (BRD) when no dolphins were sighted with feeding cores - one example from the bootstrapping procedure (2000 repetitions).

		Depth (m)	Distance (m)	Turbidity (m)	Salinity (ppt)	Water Temp (°C)	Birds	Boats	Shrimpers (#/cell)
N		183	183	183	183	183	183	183	183
Median		-9.093	9774.3	.500	22.000	25.400	12.990	.9996	.000
Chi-Square		10.518	.035	4.548	.945	.143	5.266	2.892	2.622
df		1	1	1	1	1	1	1	1
P		.001	.851	.033	.331	.705	.022	.089	.105
Yates' Continuity Correction									
	Chi-Square	9.576	.002	3.937	.678	.053	4.606	2.409	1.921
	df	1	1	1	1	1	1	1	1
	P	.002	.968	.057	.410	.818	.032	.121	.166

was usually above 40%. However, these results are not directly comparable because quantification of behavior in mixed groups was performed somewhat differently. I observed feeding in association with shrimp vessels in almost 35% of feeding groups, which is similar to the proportion (42%) obtained by Henningsen (1991) in an area covering GB and adjacent waters. This observation illustrates that bottlenose dolphins in GB often feed opportunistically, taking advantage of readily available prey. This behavior had been documented in GB (Fertl 1994a), but her study focused on quantifying the percentage of identified individuals in mother-calf groups.

Bottlenose dolphins in the wild have flexible feeding habits and exploit new sources of food made available by human activities. Bottlenose dolphins associate with fisheries, in particular bottom-trawling (Fertl and Leatherwood 1997), and in some areas, habituated dolphins even come to shore to receive handouts of fish (for example, Connor and Smolker 1985).

Galveston Bay is the most productive commercial fishery in Texas, with shrimp being the most intensively harvested (GBEP 2002) and Galveston ranking number 15 in commercial landings by value in the U.S. (NOAA 2004). In addition to this supplemental food source available to dolphins feeding in association with shrimpers, the most important prey species for bottlenose dolphins in estuaries (Atlantic croaker, *Micropogonias undulatus*, pinfish, *Lagodon rhomboids*, and spot, *Leiostomus xanthurus*) are very abundant in the GB and remain plentiful year-round (Nelson 1992, Nelson and Monaco 2000). Thus, arguably GB constitutes a major feeding ground for local and transient bottlenose dolphins.

Two of the five locations surveyed in this study accounted for 94% of the observed feeding groups. It appears that the Galveston Ship Channel and Bolivar Roads represent the main feeding areas for bottlenose dolphins in the Lower Galveston Bay. The only other area in Galveston Bay known to experience regular occurrence of dolphins is a significant distance away in the West Bay and San Luis Pass (Maze 1997, Henderson 2004), located near the opposite, or south-southwest, end of the 51.6-km-long barrier island of Galveston. However, there is growing evidence that this represents a much

smaller community (*sensu* Wells *et al*. 1999) of fewer than 50 dolphins (Maze 1997, Maze and Würsig 1999, Henderson 2004). Furthermore, aerial surveys of the entire Galveston Bay region confirm the observation in the present study that the Lower Galveston Bay, towards the north/northwest end of Galveston Island, is the region where the highest density of dolphins occurs (Henningsen 1991, Henningsen and Würsig 1991). Individual identification of dolphins from the Lower Galveston Bay has been and continues to be conducted and not only may provide a useful estimation of the abundance of dolphins in this area but also may permit determination of whether dolphins that feed in association with shrimp vessels tend to be resident individuals, as hinted by Fertl (1994a). The latter study showed that 74% of the identified dolphins that fed in association with shrimpers, were probably residents as they were re-sighted at least once in the course of the study.

In the present study, Bolivar Roads experienced a higher mean encounter rate than did Galveston Ship Channel, indicating that more dolphins feed in this area at any given time. However, a high proportion of the feeding groups were sighted in GSC. This discrepancy may be explained by the lower group size observed in GSC than was seen in BRD. The most frequently observed group size in GSC was two dolphins compared to six individuals in BRD.

Spacing and relative orientation among group members are important elements of the sociality of cetaceans (Norris and Dohl 1980, Shane *et al*. 1986). It is possible that in a constricted channel such as GSC, larger group size would hamper dolphins in maintaining optimal social distances. GSC averages a depth of 6.9 m, is 2 km long, and in most parts is less than 500 m wide whereas BRD is 4 to 5 times wider and on average 6.6 m deep. Thus, I suggest that width of area through which dolphins can travel may be an important determinant of delphinid group size.

Food availability may also determine group size (Würsig 1978). Hence, another explanation for the smaller group size in GSC is that foraging may be less cost-effective for larger groups. If so, we might expect that when shrimp vessels were present in GSC, the group size would be larger than when they were absent. Although, Fertl (1994a)

found that groups feeding in association with shrimpers were smaller, this could have resulted from inflated size of groups not feeding in association with shrimpers. Since the latter also included groups feeding in BRD, which I found are larger than those in GSC.

Although size of bottlenose dolphin groups is often related to behavior (Shane *et al*. 1986), the average feeding group size (7 dolphins) found in this study is similar to that reported for bottlenose dolphins in Gulf of Mexico estuaries (3 to 7 individuals) (Grüber 1981, Henningsen 1991, Bräger 1992). In part, this may result from the fact that feeding is a major activity in all estuaries. In adjacent coastal waters of GB, group size tends to be larger (Henningsen 1991).

The higher mean encounter rate found in BRD is not an artifact caused by a wider expanse in BRD than in GSC, which would increase the range of detection of groups in the former area. In the present study, a constant search distance (200-m radius) was kept and all the groups that were beyond this distance were identified with GIS and excluded from the analysis. This procedure was performed to ensure equal detectability of dolphins among all surveyed locations regardless of their size.

The observed preference of dolphins for the southern part of the bay cannot be accounted for strictly by the presence of shrimp vessels in the Galveston Ship Channel, since commercial fishing is almost non- existent in BRD -- a main feeding area -- in contrast to HSC, a major trawling ground of very low feeding density. The increasing trend of fish size from smaller in the north to larger in the south is a plausible explanation for an apparent preference for the southern region (Patillo *et al*. 1995). Furthermore, the diversity of species is also higher in the area encompassed by GSC and BRD (Nelson and Monaco 2000).

Important demersal fish species that comprise the diet of bottlenose dolphins in estuaries such as Atlantic croaker, pinfish and spot (Barros and Odell 1990, Barros and Wells 1998, Gannon and Waples 2004), are most abundant in seawater and mixing salinity conditions (Nelson 1992). Hence, it is possible that the assemblage of fishes that bottlenose dolphins prey on preferably occurs at higher salinities. This hypothesis is

supported by the higher salinity measured in CFDs compared to conditions of lower salinity in regions where no dolphins were detected.

Man-made structures of substrates such as quarry rock boulders offer food supply and shelter from predators and from tidal currents serving as an aggregating device for fish (Bohnsack and Sutherland 1985, Bohnsack 1989, Pickering and Whitmarsh 1997, Walker *et al*. 2002). Thus a higher density of dolphin feeding would be expected along the jetties. However, this study found a clear preference by dolphins for specific sites along the jetties. In fact, even at the small scale of GSC-BRD (43 km^2), the distribution of their feeding events was highly clustered.

Several hydrographic conditions typical of deep channels, jetties and strong current zones promote the aggregation of fish. For example, fish experience more stable salinity and temperature conditions on the bottom of deep channels (Patillo *et al*. 1995). Tidal fronts lead to higher concentrations of nutrients and phytoplankton and create favorable feeding conditions for a variety of predators, including seabirds and dolphins (Dustan and Pinckney 1989). These zones of high turbidity may also be used to avoid predation by visual hunters. Bottlenose dolphins can use echolocation to detect and capture their prey, thus taking advantage of this aggregation of prey. In addition, bottlenose dolphins feed against the current, a counterforce thought to act as a boundary limiting fish movements and hence facilitating their capture. This behavior commonly occurs under causeway bridges (Shane 1990).

I posit that the main CFDs constitute areas where fish are aggregated or where dolphin capture of prey is facilitated by moderate to strong currents. The area of GSC3, at the mouth of the GSC channel, is a zone of confluence, where fronts are often visible on the surface. The area of BRD8 is located along a break in the jetty, a structure which likewise creates high turbulence. Moreover, GSC3 and BRD10 are the end points of the ferry crossing. Ferries stir up the bottom and may have a similar restricting effect as do currents, or their undersea wake may simply dislodge fish from the bottom.

This study shows that CFDs may shift, expand or contract, and some may even disappear with shifting seasons and times of day. In general, however, the main CFDs

observed in this study were stable. The mean center of the combined CFDs shifted from Bolivar Roads in the warm season to Galveston Ship Channel in the cold season. The highest number of fish species in the GB occurs between March and October (Nelson and Monaco 2000), which overlaps generally with the warm season (April to November). I hypothesize that: (1) the association of higher density with the warm season results from an increase in transient dolphins that primarily use BRD and (2) in the cold season, mostly residents occupy the bay and primarily use GSC, possibly depending more at that time on feeding in association with shrimp vessels. It is beyond the scope of the present study to determine whether higher feeding density results from an increase in the number of dolphins in the bay or, alternatively, from a higher degree of clumping. However, previous studies of occurrence patterns of dolphins in GB have reported an increase in dolphins from spring to fall (Henningsen 1991, Bräger 1992, Fertl 1994a).

The set of variables that was useful in predicting CFD were, in decreasing order of relevance, distance to the Gulf of Mexico, surface water temperature, depth, number of boats, and temperature season.

Distance had the strongest effect, with the highest feeding densities found closer to the entrance of the estuary. Bottlenose dolphins have wide and variable home ranges. Resident dolphins from Sarasota Bay, Florida, have a home range that extends along 40 km of coastline (Barros and Wells 1998). GSC and BRD are less than 15 km from the Gulf waters. Assuming a home range for resident dolphins in GB comparable to Sarasota Bay residents, my results suggest that most observed dolphins have a home range that includes both GB and the nearshore waters of the Gulf. The higher density predicted during the warm season could be an indication that influxes of dolphins occur either because of changes in home range or due to a transitory use of the bay by migrating dolphins.

An increase in boats was associated with an increase in CFD. Boats may have direct and indirect effects on prey distribution. Stationary boats, like many other floating objects, may lead to aggregation of fish that seek shelter from predators. Likewise,

recreational vessels engaged in sport fishing attract fish using bait. As mentioned earlier, ferries and bottom trawlers may contribute to exposing and stunning fish, making them vulnerable to predation. In this study we cannot evaluate whether the association with boats is spurious (i.e., simply resulting coincidentally from the higher occurrence of recreational fishing in favorable feeding areas) or whether the presence of the boats themselves may be influencing prey. This question will be addressed in future studies that classify and catalogue the number of boats by type (recreational vessel, ferry boat, shrimp vessel, etc.) and activity (stationary, fishing, traveling).

Deeper waters were conducive to higher dolphin density. Depth was also the most prominent difference between the average environmental conditions in CFDs and those measured in GSC and BRD when no dolphins were detected.

Interestingly, temperature appears to have opposite effects at different time scales. Although the warm season was associated with higher CFD, higher surface water temperature was negatively associated with density. Since GB is a wind-driven estuary with strong mixing, it is unlikely that this discrepancy could be explained by vertical stratification of water temperature. Alternatively, it could result from different temporal scales of measurement. Season is a much coarser measure of water temperature than daily temperatures as measured directly with warm season encompassing over 50% of the total yearly variation. Hence, the observed relationship to dolphin density could be related to unmeasured factors such as fluctuations in prey abundance that influence feeding dolphin density.

This study evaluates only the factors that appear to influence the very high density of feeding dolphins in areas defined as “CFD”. Subsequent investigations may find that different factors exert strong influences if the density range is broadened by lowering the cutoff density in the definition of CFD.

It is clear that several factors, possibly acting in concert, are involved in determining high feeding density. The goal of this study was to evaluate the relevance of this group of variables and select a parsimonious model rather than to explore possible effects of multiple interactions.

CONCLUSIONS

In estuaries, dolphins probably expend more energy locating their prey than capturing it. The availability of predictable sources of food for bottlenose dolphins is likely to reduce the foraging search time and significantly increase their foraging efficiency. In the GB, such food resources may be provided by shrimp vessels, ferries, recreational boats and tidal fronts or zones of turbulence near man-made structures such as jetties.

This study corroborates that feeding behaviors of coastal bottlenose dolphins occur mainly in small groups. In addition, the study shows that feeding group size is smaller in narrow channels. More importantly, the study illustrates that bottlenose dolphins exhibit preferences for specific feeding sites. At the scale of this study, the CFDs showed great stability with minor shifts between seasons. The study highlights several factors that in estuaries may play major roles in determining CFD location and shows that taking human activities into account is necessary to understand habitat use in highly modified environments. The management of fish stocks requires not only monitoring of commercial and recreationally valued species but also of species that serve as indicators of environmental degradation (i.e. indicators of environmental stress) and those that have an important ecological role (i.e. key predator or prey) (Nelson and Monaco 2000). Bottlenose dolphins respond rapidly to changes in the environment and prey upon a variety of fish species. One of the bottlenose dolphin main target prey species -- the Atlantic croaker -- is designated as indicator of environmental stress (Nelson and Monaco 2000). Therefore, monitoring the density of CFDs may serve as an indirect measure for assessing fluctuations of fish assemblages. This may be particularly beneficial in areas such as the site of the present study, the Galveston Bay estuary, that have been classified as Essential Fish Habitat, a designation which carries an obligation to monitor fish species.

CHAPTER IV

SUMMARY

This study shows that even in a dynamic system such as estuaries, habitat preferences can be determined in the patterns of distribution of bottlenose dolphins. In Chapter II[18], I investigated which environmental factors were most strongly correlated with bottlenose dolphin distribution. In Chapter III[19], I focused on feeding behavior and the environmental characteristics of the major feeding sites.

Both natural and anthropogenic environmental variables were useful in predicting bottlenose dolphin distribution. At the scale of the entire bay, almost all of the initial variables were retained as useful predictors. The strong negative effect of distance to the Gulf of Mexico suggests that the home range of the dolphins that use the bay extends into the Gulf waters.

Since feeding consumes a major proportion of the activity of dolphins in the Galveston Bay, it is likely that many of the environmental features I found to be correlated with dolphin occurrence are related to aggregation of prey. For instance, dolphins were more frequently associated with deep channels, which offer more stable conditions for benthic fish species. Since bottlenose dolphins in estuaries feed mostly on benthic fish species, the dolphins' association with deep channels strongly supports the hypothesis that this occurrence is mostly determined by abundant feeding conditions. Among the five locations surveyed, the areas with more than 85% of the occurrences are almost entirely channels, many of them maintained by dredging. The positive correlation between occurrences and number of seabirds is also likely an indication of better feeding conditions in those areas.

Although bottlenose dolphins avoid boat traffic in certain estuaries, the positive correlation of dolphin occurrence with the Galveston Bay deep channels suggests that under certain ecological conditions, such as abundant food resources, the benefits of

[18] Fine scale environmental predictors of bottlenose dolphin distribution in the Galveston Bay, Texas
[19] Environmental predictors of bottlenose dolphin core feeding densities in the Galveston Bay, Texas

foraging may outweigh the presumed negative impact of boat traffic. Liret (2001) also found that a harbor with intense boat traffic is primary habitat for bottlenose dolphins, in this case for resting. In the latter study, the reaction of bottlenose dolphins to boats was monitored showing the majority of the interactions to be null reactions. This contrasts to other studies (Janik and Thompson 1996, Nowacek *et al*. 2001, Hastie *et al*. 2003) that report changes in behavior associated with boat traffic.

This study shows how spatial scale determines the model obtained for occurrence of bottlenose dolphins, revealing different influential factors among locations and throughout the bay. Of the three locations (BB, BRD, and GSC), only in GSC were both anthropogenic variables -- number of boats and shrimp vessels -- required to successfully model occurrence.

Bottlenose dolphins are generalists and feed opportunistically, switching to the most abundant source of food. I found that about 20% of the feeding events were in association with shrimpers. Since shrimpers operate in the Galveston Bay throughout the year and the occurrence of dolphins was positively correlated with number of shrimpers, I hypothesize that dolphins regularly use this food source. This phenomenon may constitute another example of how abundance of food resources shapes behavior in cetaceans. Future studies that identify the individual dolphins that are year-round residents may be able to more precisely document the extent of the dependency of certain individuals on shrimp vessels.

Feeding was highly clustered in the two main areas of occurrence, which together account for 94% of the feeding groups. The location of the sites of high feeding densities is consistent with features that promote aggregation of fish. At the level of the entire bay, five variables were important predictors of high feeding densities and, as was found for occurrence, the number of boats was an influential parameter. This observation further underscores the need to address anthropogenic variables in habitat studies. Core feeding densities in the warm season (April to November) were higher than in the cold season. Compared to the conditions in the entire bay when no-sightings were made, the high feeding density areas were closer to the Gulf of Mexico, tended to be deeper, and

registered higher salinity and higher surface water temperatures, and were associated with higher numbers of boats and birds. The locations of these core feeding areas in zones of confluence suggest that currents and tidal fronts may play an important role in aggregating prey. Interestingly, Liret (2001) found that off the Sein Island, Brittany, bottlenose dolphins choose shallow waters for feeding, in marked contrast to my observation of their preference for deep waters in the Galveston Bay. A common denominator in both these studies regarding feeding behavior is that the dolphins selected areas of high turbulence. In her study, Liret (2001) found that strong currents around submersed rocks comprise one of the main feeding sites. In the Moray Firth, Scotland, the higher abundance of bottlenose dolphins feeding at the mouth of the estuary has been proposed to result from a bottleneck restricting the dispersion of fish (Wilson *et al*. 1997, Hastie *et al*. 2004). Because Bolivar Roads is the main route to the Gulf of Mexico, a similar effect may generate favorable feeding conditions for bottlenose dolphins and seabirds. However, finer scale current patterns probably are responsible for the segregation of feeding habitat within this area.

The largest area among the main core feeding sites was approximately 3 km^2. Few studies have analyzed habitat use of bottlenose dolphins at a fine scale (i.e. = 500 m). A detailed study spanning several years (Liret 2001) found that a small population of bottlenose dolphins off Brittany feeds in an area of 3.4 km^2. Since in the present study, the core feeding area represents only high feeding densities, the total feeding area in Galveston Bay is at least 43 km^2, corresponding to Galveston Ship Channel and Bolivar Roads. This difference is probably due to the higher number of dolphins in the Galveston Bay, estimated as 200 resident dolphins, which is greater than the population in Sein Island by at least a factor of ten.

Estuaries typically have a patchy distribution of food resources, and thus finding discontinuity of the core feeding sites is not surprising. However, if the distribution of food resources were unpredictable, we would not expect to see such apparent stability for the main core feeding sites. I suggest that by associating with these locations, bottlenose dolphins may benefit in at least two ways: reduction of search time and

reduction of hunting time. While search time is diminished by the higher density of prey, the reduced hunting time results from a combination of physiographic conditions that facilitate capture of prey. Bottlenose dolphins have a remarkable plasticity of behavior, as shown by the diverse techniques used in hunting even within a regional scale. However, little is known about decision-making processes that govern foraging. Hence, by identifying stable and rich food sites, future studies may test whether bottlenose dolphins behave more as Bayesian foragers or as prescient foragers. The latter tend to use food resources more optimally than Bayesian foragers. Prescient foragers rely on memory to preferentially exploit stable rich food patches. In addition, they can adjust the pattern of exploitation when patch quality changes, for example using visual or acoustic cues to estimate patch richness prior to exploitation (Alonso *et al.* 1995, Giraldeau 1997). One possible approach to address this question would be to evaluate the relationship between the time that dolphins spend in each feeding core and the abundance of prey in these locales, estimated by techniques such as fish-finding sonar (Benoit-Bird and Au 2003).

Following an integrated approach that spatially and temporally models the environmental conditions that determine dolphin occurrence and feeding patterns, I identified the areas of Galveston Bay that are important habitat for bottlenose dolphins. This approach provides insight into the main environmental features that contribute to the heterogeneous use of the habitat. This methodology, which accounts for both natural and anthropogenic variables, may be a useful model to establish boundaries of, and define zonation within, marine reserves based on solid criteria related to the biological and ecological value of the area.

Recently, the use of focal species to devise conservation strategies has been proposed for the marine environment. Considering that bottlenose dolphins are top-predators and feed on a variety of fish -- including species identified as ecologically important due to their role in shaping marine communities -- their potential designation as focal species (in particular as indicator, umbrella and keystone species, as defined by Zacharias and Roff 2001) should not be underestimated. At first glance, bottlenose dolphins might

seem unsuitable candidates to be focal species thanks to their adaptability to different niches and, among some populations, their reduced site fidelity. However, the opposite conclusion may be reached if the particularities of their feeding habitat are considered.

The application to the marine environment of focal species concepts is still being debated, largely because of the higher fluidity of the environmental conditions and spatial and temporal variations of populations, communities and ecosystems (Zacharias and Roff 2001). The utility of focal species is dependent on careful definition of specific conservation goals, as well as by precise consideration of what types of focal species appear to be most appropriate, such as indicator, keystone, umbrella or flagship species. To define marine reserves with the goal of preserving an excellent representation of marine habitats, composition indicators (i.e., indicators of a certain habitat) have been proposed as the most efficient tool (Zacharias and Roff 2001).

Several studies -- extensively reviewed by Reeves (2002) and Hoyt (2005) -- have suggested the importance of considering cetacean distribution to help establish marine protected areas and, in particular, to identify critical habitats based on cetacean patterns of habitat use. Studies of bottlenose dolphin habitats have been used to help design protected areas in, for example, Moray Firth, Scotland (Wilson *et al*. 1997) and Brittany, France (Liret *et al*. 1996, Liret *et al*. 1999). The study of habitat use by multiple cetacean species led to proposing the conservation of a submarine canyon (the Gully) off the east coast of Canada (Hooker *et al*. 1999). That study demonstrated the association of cetacean occurrence with depth and sea surface temperature, and provided additional evidence of the importance of considering physiographic features that foster biodiversity.

In view of the increasing interest in establishing marine protected areas (MPA's) as an ecosystem-based management approach to conservation, and considering how a recognition of the crucial role of marine megafauna, including marine mammals, may assist in designing successful MPA's (Hooker and Gerber 2004), the present study provides an example of how zonation (i.e., defining different levels of conservation) might be determined. Moreover, cetaceans are undoubtedly one of the most charismatic

taxa and thus may be used as flagship species, a powerful tool to assist implementation of MPA's.

The model used in this study reveals a pattern of dolphin occurrence and feeding sites related to environmental conditions that should be tested further for its applicability to other years and sites. Initially, such a study might be undertaken by using data already collected in Galveston Bay during subsequent years. Ultimately, it would be desirable to undertake additional studies seeking to predict dolphin occurrence using environmental conditions observed in other estuaries where long-term longitudinal studies of bottlenose dolphins already have been carried out. However, it should be recognized that different models may yield different results, and thus it is advisable that other modeling techniques be employed as well for further exploration.

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Selected Publications:

- Moreno, P., C. Kamminga and A. Cohen Stuart. 2003. Click sounds produced by the Amazon River dolphin (*Inia geoffrensis*) during sexual interactions in captivity *in* Echolocation in Bats and Dolphins, University of Chicago, p. 419-425.
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